

The American Midland Naturalist

Devoted to Natural History

Primarily that of the Prairie States

Founded by J. A. Nieuwland, C.S.C.

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Theodor Just, Botany

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Errata Graviosa

- P. 542, line 29, read:
 "whether it is a *Lepidophyllum* (*Cantheliophorus*) or a *Lepidostrobus*. He then proposes"
- P. 797, lines 2 and 4 from bottom, read:
 "molar-premolar series."
- P. 798, line 10, read:
 "Master of Christ's College, Cambridge, has done Ray the justice so long overdue him."
- P. 798, line 16, read:
 "its day exercised a considerable influence. I am not sure that Dr. Raven has been"
- P. 799, lines 22 and 23, read:
 "history of John Ray and his work. It remains but to add that the Cambridge University Press has produced the book with the usual good taste, and consummate presswork, which"

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NO. 1

Studies in *Phacelia* — a Revision of Species Related to *P. pulchella* and *P. rotundifolia*

John Thomas Howell

Introduction

The taxonomic problems centering in *Phacelia pulchella* Gray, *P. rotundifolia* Torr., and related species that occur in the arid regions of the southwestern United States came to my attention in 1936 when I was asked by Dr. Edward H. Graham to determine collections of *Phacelia* he had made in the Uinta Basin in northeastern Utah (cf. Graham, 1937). At that time further studies were not made because of the real paucity of herbarium collections and also because of the desire and need for even a limited amount of field experience in so critical a group.

In May, 1941, on a collecting expedition made by Miss Alice Eastwood and myself to southern Nevada and Utah, I was able not only to observe the field occurrence of a number of the species and forms in this relationship, but I was also able to obtain much-needed specimens for critical herbarium studies. This material was augmented by the gift of an even larger number of specimens from Mr. H. D. Ripley and Mr. R. C. Barneby who collected no fewer than nine of these rare species during 1941 in California, Nevada, Utah, and Arizona. In order to name these accumulated collections it was necessary to prepare a revision for the group, since nothing published was adequate.

The species included in this study belong to the subgenus *Eutoca* and are to be distinguished by the following characters: Plants chiefly annual (3 species perennial) with leaves entire to shallowly lobed, corollas tubular or tubular-campanulate, stamens shorter than the corolla, style bifid or at most parted only 1/3 its length, and capsule generally elliptic or oblong and obtuse or truncate below the terminal apiculation.

Although the group of species thus set off is a natural one for the most part, several lines of development are probably represented which center more immediately in such species as *P. demissa* Gray, *P. pulchella* Gray, *P. incana* Brand, and *P. rotundifolia* Torr. The interrelations between the several smaller groups, however, are such that none stands out clearly apart from the others and it has seemed best to present all of them in a single revision.

The group as a whole is considerably less inclusive than the section *Pulchellae* of Rydberg (1917, p. 702) which included plants with open-campanulate corollas and styles more deeply cleft (cf. *P. curvipes* Torr. and *P. minutissima* Henderson). Since, in a general survey of the subgenus *Eutoca*, such broad limits when unrestricted by geographic boundaries would encompass entities so much more divergent than even those accepted by Rydberg, the present limits have been fixed on the basis of more approximate relationship and as a matter of convenience. Even with these more restricted limits, at least two species have been included which seem less intimately related to the remainder of the group, *P. saxicola* Gray and *P. suaveolens* Greene. For the latter, the only species in this group from as far west as the coastal drainage of California, one may search for a distant connection with such a widely distributed desert plant as *P. Lemmonii* Gray; and, for the former, even with its tardily deciduous corollas and scarcely reticulate seeds, the affinity seems to be with the present group rather than with the other species of the subgenus *Eutoca* with marcescent corollas related to the perennial *P. sericea* (Grah.) Gray. As to the relation between our group as a whole and the remainder of the subgenus *Eutoca*, I am not able to state anything at present.

Acknowledgments. The herbarium studies, which have been made in the Department of Botany of the California Academy of Sciences (CAS), have been immeasurably aided by visits to other institutions and by loans of historical and critical collections from yet other herbaria. These herbaria and the symbols used to designate them in the citation of specimens are as follows:

University of Arizona (Ariz);
 Dudley Herbarium, Stanford University (DS);
 Field Museum (F);
 Frank W. Peirson, Altadena, California (FP);
 Gray Herbarium, Harvard University (G);
 Greene Herbarium, University of Notre Dame (ND);
 Intermountain Herbarium, Utah State Agricultural College (IU);
 Missouri Botanical Garden (M);
 New York Botanical Garden (NY);
 Pomona College (P);
 Rocky Mountain Herbarium, University of Wyoming (RM);
 U. S. Dept. of Agriculture Field Station, Sacaton, Arizona (Sac);
 University of California, Berkeley (UC);
 United States National Herbarium (US).

I wish to thank the curators and owners of these collections for the privilege of studying the specimens; and, also I wish to express my sincere appreciation and gratitude to many friends who have contributed valued specimens and other assistance to my studies in *Phacelia* over a period of years.

KEY TO THE SPECIES

- A. Ovules 8—16 in each ovary.
 - B. Leaves serrate or serrate-lobed, venation prominent 1. *P. suaveolens*
 - B. Leaves entire or undulate, venation not prominent.
 - c. Stems subprostrate; leaves oblong to elliptic; flowers in dense sessile clusters in forks of branches; seeds spongy-pitted and fibrillose 2. *P. cephalotes*

- c. Stems ascending or suberect; leaves broadly ovate to orbicular; flowers not capitate-congested; seeds pitted.3. *P. demissa*
- A. Ovules 20—200 in each ovary.
- D. Pubescence of stems finely glandular-puberulent, the hairs generally numerous, pubescence not hirsutulous or villous. (See also *P. Peirsoniana* which is sometimes more glandular-puberulent than glandular-villous.)
- E. Fruiting sepals not very unequal, the widest less than 2 mm. wide (or if 3 mm. wide the corolla more than 10 mm. long).
- F. Pedicels generally 3—15 mm. long; corollas 7—15 mm. long, or if only 3—7 mm. long, then the ovules only 20—40 in each ovary; corolla-scales 1.5—3 mm. long; ovules generally 20—50.
- G. Pedicels mostly 5 mm. long or less, shorter than the fruiting calyx.
- H. Corolla 7—15 mm. long; filaments sparsely hairy; style sparsely hirsutulous below the middle.4. *P. pulchella*
- H. Corolla 3—4.5 mm. long; filaments glabrous; style sparsely hairy at very base.5. *P. indecora*
- G. Pedicels mostly 5—15 mm. long, longer than the fruiting calyx.
- I. Corolla (9—) 10—15 mm. long; ovules 36—43.6. *P. glechomifolia*
- I. Corolla 5—9 mm. long; ovules 20—24.7. *P. filiformis*
- F. Pedicels very short, 2 mm. long or nearly lacking; corollas 4—6 mm. long; corolla-scales 1.5 mm. long or less; ovules (70 or) 90—140.8. *P. Lemmonii*
- E. Fruiting sepals markedly unequal, the widest 2.5—4 mm. wide and sometimes foliaceous; pedicels 2 mm. long or less; corollas 5—6 mm. long; corolla-scales small, 1 mm. long; ovules 30—43.9. *P. Parishii*
- D. Pubescence of stems glandular-villous or glandular-hirsutulous, generally with non-glandular hairs intermixed.
- J. Leaves oblanceolate-spatulate; corolla marcescent; seeds shallowly reticulate or nearly smooth, less than 0.5 mm. long.10. *P. saxicola*
- J. Leaves oblongish to round; corolla not marcescent; seeds pitted, 0.5—1.3 mm. long (or only 0.3 mm. long in *P. rotundifolia*).
- K. Plants annual; corolla 3—10 mm. long.
- L. Plants slender, leafy near the base, leaves elliptic-oblong to ovate; pedicels longer than the fruiting calyx, the lower pedicels 6 mm. long or more; ovules about 20.
- M. Leaves frequently serrate; pedicels glandular but not villous; corolla-scales reduced to a line or obsolete; style glabrous, 2 mm. long.11. *P. Barnebyana*
- M. Leaves entire; pedicels villous- or hirsutulous-glandular; corolla-scales narrow but widened gradually upward, 1—1.25 mm. long; style hirsutulous to the middle.12. *P. nevadensis*
- L. Plants usually more robust, leafy throughout, leaves round or nearly so (except in *P. incana*); pedicels usually shorter than the fruiting calyx, the lower pedicels 6 mm. long or less (rarely longer in *P. Peirsoniana*); ovules more than 30 (or sometimes less in *P. incana*).
- N. Leaves entire, elliptic to ovate.13. *P. incana*
- N. Leaves repand-crenate to saliently dentate-lobed, broadly ovate to round.
- O. Corolla 3—5 mm. long, white or pale lavender.
- P. Leaves repand-crenate or dentate, mostly 1.5—3.5 cm. in diameter; stems densely glandular-puberulent or glandular-villous, scarcely hirsutulous; corolla-scales 1—1.5 mm. long.14. *P. Peirsoniana*
- P. Leaves prominently and coarsely toothed or radiately crenate-lobed, mostly 0.5—2 cm. in diameter; stems hirsute and glandular; corolla-scales 0.5 mm. long.15. *P. rotundifolia*
- O. Corolla (6—) 7—10 mm. long, violet.16. *P. mustelina*
- K. Plants perennial; corolla 10—14 mm. long.

- q. Flowering stems arising each year from a low dense cushion of numerous abbreviated leafy stems; pedicels abruptly deflexed at base in fruit; ovules 50—70.17. *P. geraniifolia*
- q. Flowering stems arising from a few-branched suffrutescent base; pedicels not deflexed; ovules about 200.
- r. Older stems covered with white, non-glandular, velvety hairs; leaves generally about 1 cm. in diameter; lower pedicels to 1.5 cm. long; lower part of style sparsely hairy.18. *P. perityloides*
- r. Older stems glandular-pubescent; leaves generally 2—3 cm. in diameter; lower pedicels to 3.5 cm. long; style and lower part of branches glandular and hirsutulous19. *P. laxiflora*

Taxonomic Treatment

1. PHACELIA SUAVEOLENS Greene, Pitt. 1:223 (1888)

Plants annual, more or less glandular and hirsutulous and fragrant-scented, 0.5-4 dm. tall, stems erect or somewhat spreading, simple or few-branched at the base, the stems substrictly or fastigately erect or somewhat spreading and ascending; leaves rather equally distributed, oblong to elliptic or ovate, 1-6 cm. long, 0.5-3 cm. wide, serrate to shallowly serrate-lobed, the lobes acute or obtuse, sometimes serrulate, apex of leaf obtuse or subacute, base cuneate or rounded, venation prominent with veins impressed on the upper surface, pubescence on the upper surface appressed and strigillose, below more spreading and glandular, petioles 0.2-3 (or 4.5) cm. long; racemes sessile or shortly peduncled, 2-7 cm. long, the lowest flowers distant, the uppermost crowded, pedicels 1-2 mm. long, or the lowest up to 5 mm. long; sepals in flower 5 mm. long, 0.6-1.5 mm. wide, oblanceolate to broadly oblanceolate-spatulate, subacute, hirsutulous and glandular, in fruit becoming 6-8 mm. long, 1-3 mm. wide; corolla tubular-campanulate with spreading limb, 7-14 mm. long, 5-10 mm. across, the lobes 2 mm. long in the larger flowers, the limb lavender to rose-purple, the tube yellow; corolla-scales attached to filaments for longer or shorter distances, the upper part very narrow, 1-2 mm. long in one flower; stamens more or less unequal, 3-5 mm. long, filaments glabrous, anthers oblong 0.6-1 mm. long; style and branches 3-4 mm. long, the branches 0.5-1 mm. long, the style tuberculate-glandular and hirsutulous to above the middle or the hirsutulous hairs only near the base; ovary 1 mm. long, long-hirsute, ovules 8-16; capsule oblong-elliptic or ovate, 3-4 (or 5) mm. long, acute or obtuse below the terminal apiculation; seeds brown or blackish, acute or obtuse, coarsely pitted, 1 mm. to nearly 2 mm. long.

KEY TO THE VARIETIES OF *P. SUAVEOLENS*

- Corollas mostly 10 mm. or less long, the limb lavender or pinkish lavender; central Californiavar. *typica*
- Corollas mostly 10 mm. or more long, the limb rose-purple; southern California.....var. *Kechii*

1a. *Phacelia suaveolens* Greene var. *typica*, nom. nov.

Petioles of lowest leaves generally 2-3 cm. long; corollas 7-11 mm. long; ovules 10-16.

A rare plant of scattered distribution in central California, Coast Ranges from Lake County south to Marin and Contra Costa counties and Sierra Nevada foothills in Amador Co., 1000 to 4000 ft. May-August.

Collections. S.E. slope of Mt. Konocti, Lake Co., *Carter No. 354* (CAS, UC); summit of Middle Peak, Mt. St. Helena, Napa Co., *Jackson in 1930* (CAS); near the summit of Mt. Tamalpais, Marin Co., *Heller No. 8391* (CAS, DS, F, M, P); Black Hills, Mt. Diablo, *Bowerman No. 2078* (CAS); Lone, Amador Co., *K. Brandegee in 1910* (UC), *Hoover No. 2419* (CAS, DS, UC).

Phacelia suaveolens occurs most commonly in open places in the chaparral and is sometimes locally abundant after fires. As might be expected from such widely and distinctly separated collections as those cited above, there are some variations to be noted. Hoover's specimen from Lone has the corollas only 7 mm. long and the tall plants are fastigiately branched. Heller's collection from Mt. Tamalpais, in which the lowest branches frequently spread widely, exhibits fruiting sepals notably enlarged and corollas 11 mm. long. The type specimen which was collected by Greene at the Petrified Forest in Sonoma Co. (ND) does not exhibit the lower leaves described by Greene "with some lyrate lobes at or below the base of the main blade." A corolla of the type is 9 mm. long.

1b. *Phacelia suaveolens* Greene var. *Keckii* (Munz & Johnston),
comb. nov.

Phacelia Keckii Munz & Johnston, Bull. Torr. Bot. Club 51:298 (1924).

Petioles of lowest leaves generally 2 cm. long or less; corollas 9-14 mm. long; ovules 8-10.

Known only from the higher slopes of the Santa Ana Mts. in Riverside and Orange counties, California, 4000 to 5000 ft. May-June.

Collections. Along trail from Glen Ivy to Santiago Peak, 4700 ft., Riverside Co., *Munz No. 7056* (P, type), at about 4000 ft., *J. T. Howell No. 6611* (CAS, DS, F, G, M, ND, NY, P, UC, US); Santiago Peak, west slope of Santa Ana Mts., 4800 ft., Orange Co., *Munz No. 7763* (P); Santiago Peak, Orange Co., *Abrams No. 1839* (DS).

The characters by which *P. Keckii* and *P. suaveolens* may be distinguished are not regarded as specific in value, especially since the two plants, as Munz and Johnston remark, "are similar in gross aspect." The distributional problem involved is of special interest since the occurrence of a variant of this central Californian *Phacelia* in the Santa Ana Mts. adds one more species to the list of more northern plants which find there the southernmost limit of their distribution (cf. Munz, p. xxv, 1935; J. T. Howell, p. 239, 1936).

It may be that *P. suaveolens* does not rightly belong in this treatment of phacelias which are chiefly related to *P. pulchella* and *P. rotundifolia* and whose distribution is otherwise restricted to the arid regions of the American southwest. Greene originally described the lowest leaves with "some lyrate lobes at or below the base of the main blade," but in none of the specimens I have examined have I seen any tendency toward profound or lyrate lobing of the

leaves. Although the leaves in *P. suaveolens* are not so definitely lobed as in some forms of *P. rotundifolia* and *P. geraniifolia*, Brand (1913, pp. 104, 105) places it with species with leaves more or less pinnately parted while he places the other two with species with leaves entire ("folia integra")! In flower-structure, *P. suaveolens* resembles the other species of the *P. pulchella* group and so it has been included here.

2. PHACELIA CEPHALOTES Gray, Proc. Amer. Acad. 10:325 (1875)

P. curvipes Parry, Amer. Nat. 9: 16 (1875), nomen nudum; Gray, l.c., in synon.; not *P. curvipes* Torr. (1871).

Plants annual with stems low and widely spreading from the base, subdichotomously branching, 0.5-1.5 dm. long, glandular-villous and more or less hirsutulous, the lower internodes elongate, as much as 7 cm. long; leaves oblong and elliptic to ovate, to 2 cm. long and 1 cm. wide, entire, obtuse or subacute, hirsutulous and glandular, at base cuneate, petioles 1-1.5 cm. long; racemes nearly or quite sessile, short and densely flowered, pedicels to 2 mm. long or lacking; sepals in flower linear-oblancoelate, 4 mm. long, 0.5-0.75 mm. wide, in fruit becoming 7-8 mm. long, 1-1.5 mm. wide, linear-oblancoelate, subacute; corolla tubular, 4 mm. long, the lobes 1 mm. long, lavender, tube pale yellowish; corolla-scales minute, 1 mm. long, less than 0.25 mm. wide; stamens a little unequal, 1.5-2 mm. long, filaments glabrous, anthers oval, about 0.25 mm. long; style including branches 1.5 mm. long, the branches less than 0.5 mm. long; ovary 1.3 mm. long, ovules 8-12; capsule ovate, 3 mm. long, bristly-hairy and glandular; seeds 1.5 mm. long, oblongish, angular, acute, the coat spongy, fibrillose and dark-dotted.

Known only from southern Utah. April-June.

Collections. Washington County: valley of the Virgin River, *Parry No. 179*, May, 1874 (G, type; F, M, NY); St. George, *M. E. Jones No. 1646* (Ariz, CAS, DS, F, G, IU, ND, NY, P, UC, US); near Washington, *Eastwood & Howell No. 9151* (CAS, G, IU, NY, P, RM, US). Kane County: Kanab, *Mrs. A. P. Thompson (G), Ripley & Barneby No. 4342 & No. 4814* (CAS), *Eastwood & Howell No. 9305* (Ariz, CAS, FP, G, P, US). San Juan County: Montezuma Canyon, *Eastwood in 1892* (DS, NY, UC). Without definite locality: *Capt. Bishop in 1873* (G), in 1872 (US); *Parry in 1874* (DS, probably part of the type collection).

Although Capt. Bishop's collection is the first cited by Gray, the collection of Parry is chosen as the type since Gray cites the name that Parry gave to his plant in his "Botanical Observations in Southern Utah in 1874." From Parry's reference, one would infer that the plant grows in rock crevices but it seems to be confined to clay slopes. At both stations where it was found by Miss Eastwood and me, it grew on those peculiar clay knolls that form below the receding front of the massive red sandstone known as "vermillion cliffs." At both places, it was associated with other rare and remarkable plants among which were *Eriogonum subreniforme* Wats. and *Astragalus ampullarius* Wats. The *Astragalus* has been known heretofore only from the original collection; and no specimen of *P. cephalotes* collected between 1892 and 1941 has been seen (cf. Leaf. West. Bot. 3:137).

3. *PHACELIA DEMISSA* Gray, Proc. Amer. Acad. 10:326 (1875)

Plants annual, finely glandular-puberulent or occasionally glandular-villous, 0.3-2 dm. tall, few-branched at base and rather few-branched above, erect or the lower branches somewhat ascending, lower internodes elongate, the leaves mostly near the ends of the stems; leaves very broadly ovate to orbicular or even wider than long, mostly 1-2.5 cm. long, sparsely pubescent with glandular and non-glandular hispidulous hairs, entire or repand-undulate, obtuse, at base abruptly or gradually cuneate or truncate, petioles to 1.5 cm. long; racemes sessile, the lowest flowers distant, the uppermost crowded, mostly 1-4 cm. long, racemes rarely reduced to 1-3 flowers, pedicels 1-2 (or rarely even 7) mm. long or nearly lacking; sepals in flower linear-oblong, 2-3.5 mm. long, about 0.5 mm. wide, in fruit 5-6 mm. long, 0.66-1.33 mm. wide, linear-oblong to narrowly oblong-lanceolate or -spatulate; corolla tubular-campanulate, (3.5-) 6-8 mm. long, the limb lavender or purplish, the tube pale yellow; corolla-scales very narrow, 1-2.5 mm. long, attached to the base of the filaments; stamens 2-4.5 mm. long, filaments with a few hairs, anthers roundish, about 0.5 mm. long; style including branches 1.5-4 mm. long, the branches 0.25-1 mm. long, the style hairy below; ovary 0.5-1 mm. long, ovules 10-16; capsules 3-4 mm. long, oblong or roundish, obtuse above, apiculate; seeds oblongish or ovate, acute or obtuse, brown, 1-1.5 mm. long.

KEY TO VARIETIES OF *P. DEMISSA*

- Stems glandular-puberulent; style 1.5—2 mm. long.....var. *typica*
 Stems glandular-villous; style 2.5—4 mm. long.....var. *heterotricha*

3a. *Phacelia demissa* Gray var. *typica*, nom. nov.

P. demissa Gray, l.c.

P. nudicaulis Eastwood, Zoe 4:123 (1893).

P. Knightii A. Nels., Bull. Torr. Bot. Club 28:229 (1901).

Lower internodes usually markedly elongate, the leaves mostly near the ends of the stems; upper stems glandular-puberulent; style 1.5-2 mm. long.

Definitely known from southwestern Wyoming south through Utah to northern Arizona. The type locality is "New Mexico." May-June.

Collections. Wyoming: in cracks of clay slopes, Bush Ranch, Sweetwater Co., *A. Nelson* No. 7118 (RM, type of *P. Knightii*; NY). Utah: 5 miles east of Vernal, 5500 ft., Uintah Co., *E. H. Graham* No. 9137 (CAS); Price, Carbon Co., *Stokes* in 1898 (UC); Ivie Creek, 6600 ft., Sevier Co., *Ripley & Barneby* No. 4752 (CAS); 2 miles south of Ferron, 6200 ft., Emery Co., *Ripley & Barneby* No. 4738 (CAS, F, IU); Cisco, Grand Co., *M. E. Jones* in 1899 (CAS, DS, P), in 1890 (G); between Thompsons Springs and Moab, Grand Co., *Eastwood* in 1892 (G, M, P, UC, US, type collection of *P. nudicaulis* Eastw.). Arizona: without data, *Palmer* (US); Lees Ferry, Coconino Co., *M. E. Jones* in 1890 (P). New Mexico: without data, *Palmer* (G, type). Without data, *Palmer* in 1869 (NY).

Undoubtedly the three *Palmer* collections cited above are the same and probably came from northern Arizona rather than from New Mexico, the locality given by Gray when the species was described. The type sheet in

Herb. Gray. bears the annotation by Gray "Sent by Parry from Washington . . .," which definitely suggests that the collections are the same and that either Gray or Parry made a mistake in referring the plant to New Mexico. Wootton and Standley (1915, p. 535) stated that the type was "collected by Dr. E. Palmer in 1869, doubtless near Ft. Defiance." The specimen in Herb. N.Y. Bot. Gard. is the only Palmer collection seen that is dated. A variant in the locality datum for the type collection of *P. nudicaulis* should also be noted: whereas it is generally given as "between Thompsons Springs and Moab," the specimen at Pomona College is given as between "Thompsons Springs and Court House Wash," Court House Wash being in the vicinity of Moab.

Brand (1913, p. 105) separated *P. Knightii* and *P. demissa* by the presence or absence of hairs on the filaments, a difference which does not hold since a few scattered hairs are generally found on the filaments in this group. Although the specimen of *P. Knightii* at Herb. N.Y. Bot. Gard. is undoubtedly a part of the type collection and carries Nelson's collection number, the collector is given as W. C. Knight.

Phacelia demissa is most common in the drainage of the Green River where it seems to be a member of that peculiar and interesting association of plants confined to alkaline clay slopes. Both physiologically and morphologically it seems most closely related to *P. cephalotes*.

3b. *Phacelia demissa* Gray var. *heterotricha*, var. nov.

A var. *typica* differt: internodis prope basin raro elongatis, planta plerumque aequabiliter folifera, caulibus superioribus glanduloso-villosis; stylo (2.5-) 3-4 mm. longo.

Type: Marysvale, Piute Co., Utah, *M. E. Jones* No. 53880, June 4, 1894 (P); isotypes (M, US).

Other collections, all from Utah. Belknap, Sevier Co., *Stokes* in 1900 (DS); Marysvale, Piute Co., *M. E. Jones* in 1916 (P); Caineville, Wayne Co., *M. E. Jones* No. 5656b (P), No. 5696h (US); Hanksville, Wayne Co., *C. Parry* in 1941 (IU).

Miss Stokes' 1900 collection of *P. demissa* var. *heterotricha* is recorded from Wadsworth, Washoe Co., Nevada, June 19 (NY, UC, US) and from Belknap, Sevier Co., Utah, June 12 (DS). Undoubtedly these plants are all part of the same collection and were made at the latter locality, Belknap, Utah. No other collection of *P. demissa* has ever been reported from Nevada (cf. Brand, 1913, p. 251) and the vesture of the stems and leaves immediately allies the plants to the heterotrichous variant of *P. demissa* found in that part of the southern Wasatch Mts. centering in Marysvale, Piute Co.

4. *PHACELIA PULCHELLA* Gray, Proc. Amer. Acad. 10:326 (1875)

Plants annual, openly and widely branched or the branches ascending and subfastigiate, 0.5-2 dm. tall, leafy throughout; stems without villous or hirsutulous hairs, clothed with a fine glandular puberulence of short capitate-

glandular hairs; leaves glandular and somewhat hirsutulous or scabridulous, oblong to ovate or orbicular, mostly 0.5-2.5 cm. long and 0.5-1.5 cm. wide, obtuse, truncate or shortly cuneate at base, the margin generally somewhat revolute, entire, undulate-toothed or coarsely repand-dentate, petioles mostly 1-2.5 cm. long or the uppermost almost lacking; racemes shortly stalked, rather loosely flowered or the flowers more crowded above, pedicels 2-6 mm. long; sepals in flower 3-5.5 mm. long, 0.5-1 mm. wide, oblanceolate, glandular and hirsutulous, in fruit 5-9 mm. long, 1-2 mm. wide, oblanceolate or oblanceolate-spatulate; corolla funnelform-campanulate, usually 8-11 (6-14) mm. long, 4-8 mm. wide, purple or violet, the base of the tube yellow; corolla-scales semi-ovate or narrower, 2-2.5 mm. long, mostly attached to base of the filaments; stamens 3-5 mm. long, slightly unequal, the filaments sparsely hairy near the base, anthers 0.5-0.66 mm. long; style 3.5-5 mm. long including the branches, branches 0.5-1 mm. long, the style hirsutulous to about the middle, ovary about 1 mm. long, ovules 30-50; capsule oblong or roundish, 3-5 mm. long, obtuse, shortly apiculate, finely hirsutulous; seeds oblong to nearly round, 0.5-1 mm. long, finely to coarsely pitted, brown.

Phacelia pulchella is a part of a complex of entities which seem to have originated on either side of the canyon of the Colorado River in Nevada, Utah, and Arizona. North of the canyon typical *P. pulchella* grows in a highly specialized environment of the mineralized soil on flats and knolls below the receding front of the red sandstone cliffs in southern Utah (cf. Leaflet West. Bot. 3:136). Westward, *P. pulchella* var. *Goodingii* is especially abundant and characteristic on the more or less alkaline alluvial slopes in southern Nevada; while to the eastward, another variant is to be found, *P. pulchella* var. *sabulonum* which grows on the sandstone plateau of the little-explored Kaiparowits region. And still further to the east, on the farther side of the Colorado River, is *P. indecora*, apparently a cliff-plant from the canyon of the San Juan River at Bluff, Utah. South of the canyon the complex is chiefly represented by *P. glechomifolia* Gray and *P. filiformis* Brand, species which differ from the plants to the north in having slender elongate pedicels. Nothing is known of the habitat of *P. glechomifolia*, a rare plant to the west of the Coconino Plateau in Arizona, but *P. filiformis* is essentially a plant of cliff-shaded ledges in the Grand Canyon to the eastward.

All of these entities are closely related and undoubtedly represent the segregation of various genetic strains, either geographically or physiologically, as a result of the uplift of the Kaibab-Coconino highland and the attendant carving of the Grand Canyon by the Colorado River. The highly varied topography and diversified edaphic conditions that have resulted from the orogenic activity in the latter part of the Tertiary in the American Southwest provide numerous niches in which the parts of a variable complex such as this may become isolated and persist. Although some of the members of this group now appear to be quite stable and distinct, yet others still exhibit that sort of variation associated with unstable or varying genetic constitution, and such are believed to represent groups of incipient entities in which evolutionary processes, both hereditary and environmental, are at present active.

KEY TO THE VARIETIES OF *P. PULCHELLA*

- A. Leaves usually entire or repand; corolla-limb purplevar. *typica*
 A. Leaves usually crenate or dentate, sometimes saliently so; corolla-limb violet.
 B. Capsule oblong, 4—5 mm. long; seeds 40—50, 0.5—0.75 mm. long.....
var. *Gooddingii*
 B. Capsule elliptic to roundish, 3—4 mm. long; seeds about 30, 1 mm. long.....
var. *sabulonum*

4a. *Phacelia pulchella* Gray var. *typica*, nom. nov.

P. pulchella Gray, l.c.

P. pulchella f. *luteola* Brand, Das Pflanzenr. IV. 251:117 (1913).

P. pulchella f. *rubella* Brand, l.c.

An elegant and delicately branched plant with stems and leaves frequently purplish-tinged, 0.5-2 dm. tall; leaves generally entire or subentire; pedicels 3-6 mm. long; calyx in fruit 5-7 long; corolla-limb purple; ovules 40; capsule oblong, 3.5-4 mm. long; seeds about 0.5 mm. long.

Sandy or gravelly flats and "gypseous clay knolls" in southwestern Utah and northwestern Arizona, 3000 to 6000 ft. April-June.

Collections. Utah: near St. George, Washington Co., *Parry No. 182* (G, type; F, M, P), *Eastwood & Howell No. 9145* (Ariz, CAS, G, NY, P, RM, US); near Shivits Village, Washington Co., *Eastwood & Howell No. 9086* (CAS, DS, US); Rockville, Washington Co., *Eastwood & Howell No. 9325* (CAS, G); La Verken, Washington Co., *M. E. Jones No. 5183r* (P); 2.5 miles west of Hurricane, Washington Co., *Maguire No. 20484* (CAS, IU); 5 miles north of junction, Mt. Carmel Highway, 6100 ft., Kane Co., *Maguire et al. No. 12301* (IU, M, UC); toward Jepson Springs, 18 miles east of Kanab, Kane Co., *Ripley & Barneby No. 4834* (CAS). Arizona (Mohave Co.): north of Wolf Hole, *Peebles & Parker No. 14761* (G, Sac), *Peebles & Parker No. 14733* (CAS, NY, Sac), *Benson No. 42* (UC); high plateau between Short Creek and Toroweap P.O., *Hilend in 1932* (CAS); north side of Mokiak Pass, *Ripley & Barneby No. 4310* (CAS).

Variation in the sizes of flowers is considerable as is shown by collections made by Maguire: in *No. 20484*, corollas are as long as 14 mm., and in *No. 12301*, they are as short as 6 mm. The former is regarded as a "giant" form and is discussed under var. *Gooddingii*. The latter requires further field study and may be a distinct entity deserving varietal recognition. In it, however, the sizes of the flower parts, small as they are, are entirely confluent with dimensions in plants known to be typical.

4b. *PHACELIA PULCHELLA* Gray var. *GOODDINGII* (Brand) J. T. Howell

Leaf. West. Bot. 3:119 (1942)

P. Gooddingii Brand, Das Pflanzenr. IV. 251: 120 (1913).

Plant coarser and more robust, all parts a little larger than in var. *typica*, mostly 1-2 dm. tall; leaves generally coarsely repand-dentate, sometimes dentate-lobed or rarely subentire; pedicels 2-5 mm. long; calyx in fruit 6-9 mm. long; corolla-limb violet or mauve; ovules 40-50; capsule oblong, 4-5 mm. long; seeds 0.6-0.75 mm. long.

Valley flats and alluvial slopes, more or less alkaline, southern Nevada, adjacent eastern California and northwestern Arizona, 1000 to 3500 ft. April-June.

Collections. California: Mesquite Valley 10 miles northwest of Kingston, Inyo Co., Abrams No. 14271 (CAS, DS). Nevada: Las Vegas, Clark Co., Goodding No. 2307 (RM, type; G, M, NY, UC), M. E. Jones in 1905 (P), Ripley & Barneby No. 3449 (CAS), Eastwood & Howell No. 8963 (CAS, US); between Jean and Sloan, Clark Co., Eastwood & Howell No. 8933 (CAS, DS, G, P); Moapa, Clark Co., Goodding No. 2192 (G, M, RM, UC), Kennedy No. 1130 (NY, US); south end of Meadow Valley Range north of Moapa, Lincoln Co., Ripley & Barneby No. 3466 (CAS). Arizona (Mohave Co.): M. E. Jones No. 5077aj, Pierce Ferry (P), 15 miles above Pierce Ferry (US); east base of Virgin Mts. near "Redrocks," Munz No. 16666 (CAS, P); road to Grand Wash, Maguire No. 20642 (CAS, IU).

The type plant of *P. Gooddingii* Brand is somewhat more robust than any other parts of the type collection which have been examined and which are quite representative of the variant of *P. pulchella* found on the alluvial plains in southern Nevada. But more robust even than the actual type of *P. Gooddingii* is a truly giant form that was collected on the limestone ridge southwest of Crystal, Clark Co., Nevada (Eastwood & Howell No. 8987, CAS). In this the leaves are as much as 3.5 cm. long, the fruiting sepals become 9-11 mm. long, the corolla is 12-13 mm. long, and the ovules are 60-80 in each capsule. Another "giant" type of var. *Gooddingii* is represented by Munz No. 14914 (CAS, M, P) from Gypsum Cave near Las Vegas in which the corollas are as much as 15 mm. long. Occasionally larger forms also occur in var. *typica*, one such individual being a fruiting specimen on the type sheet in Herb. Gray. and another being Peebles & Parker No. 14761 (Sac), a robust form with fruiting sepals as much as 1 cm. long and 3 mm. wide; and in Maguire No. 20484 (CAS), corollas attain the length of 14 mm. While these kinds of variations are very important and should be specially noted in presenting the taxonomy of a group like this, such variants are interpreted as the effect of sporadic alteration of the genetic make-up and they scarcely deserve nomenclatural recognition unless correlated with geographic or ecologic distribution, which is apparently not the case here.

At Sacaton are two specimens collected by R. H. Peebles (along trail, Havasu Canyon, Coconino Co., Arizona, No. 15007) in which the pedicels are up to 1 cm. long. The plants are intermediate between *P. pulchella* var. *Gooddingii* and *P. glechomifolia*: the leaves have a peculiar holly-like appearance with margins conspicuously dentate-lobed and revolute, and the corollas are large and showy, 11 mm. long and about as broad across the expanded limb.

Following the original description of *P. mustelina*, Coville discusses the relationship of *P. Gooddingii* Brand and *P. pulchella* Gray (Journ. Wash. Acad. Sci. 27:197, 1937). He concludes that the two are the same, but certainly there are distinctive differences between them which scarcely fall short of being specific in value.

4c. *Phacelia pulchella* Gray var. *sabulonum*, var. nov.

Annua erecta, 1-2 dm. alta, pauciramosa; foliis crenatis vel dentatis, interdum minoribus dentibus inter maiores; pedicellis 2-3 mm. longis; calyce in fructu 5-6 mm. longo; corolla violacea; ovulis circa 30; capsula late elliptica vel suborbiculari, 3-4 mm. longa; seminibus 1 mm. longis.

Type: Herb. Calif. Acad. Sci. No. 266302, collected on hot exposed rocks, Kaiparowits Plateau, Kane Co., Utah, by Philip W. Tompkins, May 4, 1939.

The smaller rounder fruits and fewer larger seeds mark this plant as a distinct variety in the *P. pulchella* group. From the abundant reddish sand that adheres to all parts of the plant, it would appear to have grown on the massive Cretaceous sandstone which, at an elevation of from 5000 to 7000 ft., caps the greater part of the Kaiparowits Plateau (cf. map, Gregory and Moore, 1931, plate 2).

5. *Phacelia indecora*, spec. nov.

Herba annua erecta gracilis 0.8-1.5 dm. alta simplex vel pauci-ramosa ramis adscendentibus; caulibus minute glanduloso-villosis pilis patentibus glanduloso-capitatis; foliis caulinis paucis passim dispositis oblongis ad ellipticis et late ovatis 0.5-2.5 cm. longis, 0.3-2 cm. latis, sparse hirsutulis glandulosisque obtusis apice anguste et late cuneatis basi repandis vel prominenter dentatis ad usque dentato-lobatis paululum revolutis margine, petiolo ad 1 cm. longo; racemis pedunculatis laxae paucifloris elongatis, floribus distantibus, pedicellis adscendentibus 2-5 mm. longis; sepalis ad anthesin paulum inaequalibus 3-5 mm. longis oblanccolato-spatulatis, in fructu paulum accrescentibus 5-7.5 mm. longis 0.75-2 mm. latis glanduloso-hirsutulis apicibus spatulatis plus minusve patentibus; corolla indecora calyce ad anthesin brevior vel paululum longiore, 3-4.5 mm. longa 2-3 mm. lata tubulato-campanulata, limbo violaceo, tubo flavescenti, lobis rotundis erectis circa 1 mm. longis; squamis 1.5 mm. longis semi-oblanccolatis ad bases filamentorum connatis; staminibus paulum inaequalibus 2.5-3 mm. longis, filamentis glabris, antheris 0.5 mm. longis; stylo et ramis 2.5-3 mm. longis, ramis 0.5 mm. longis, stylo glabro praeter basin; ovario 1 mm. longo, ovulis circa 40; capsula elliptica apiculata 3-3.5 mm. longa sparse hispidula; seminibus late subovatis brunnescentibus 0.6 mm. longis.

Type: Herb. Pomona College No. 117629, collected at Bluff, San Juan County, Utah, May 24, 1919, by M. E. Jones. Isotype in Herb. Calif. Acad. Sci.

Phacelia indecora is closely related to *P. pulchella* and bears to that species much the same relation that *P. filiformis* Brand bears to *P. glechomifolia* Gray. Although no environmental data are given by Jones with his collection, it is probable that *P. indecora* is the ecologic segregate growing in the cliff gardens on the bluffs of the San Juan River, just as *P. filiformis* is characteristic of shelving ledges of cliffs in the Grand Canyon. *Phacelia indecora* differs from

P. pulchella not only in the much smaller and inconspicuous corolla, but also in the smaller sizes of the flower parts, in the glabrous filaments, and in the nearly glabrous style.

6. PHACELIA GLECHOMIFOLIA Gray, Synop. Fl. N. Amer.
ed. 2, 2(1):417 (1886)

Plants annual, erect, 3-4 dm. tall, or in depauperate plants only 1 dm. tall, stems glandular-puberulent, mostly branching above the base, the branches rather few, erect-ascending with elongate internodes; leaves broadly ovate to roundish, 1-3 cm. in diameter, sparsely glandular and hirsutulous, crenate-dentate, the larger teeth frequently alternating with smaller ones on the larger leaves, apex obtuse, base reniform cordate or truncate, petioles to 2.5 cm. long; racemes on peduncles to 3 cm. long, laxly flowered and elongate, lowest pedicel mostly 1-1.5 cm. long; sepals in flower linear to oblong or oblanceolate, 4 mm. long, 0.33-0.75 mm. wide, glandular and hirsutulous, in fruit 6-7 mm. long, 1-1.5 mm. wide, oblanceolate-spatulate; corolla lavender or purplish, campanulate-funnelform with rather open throat and spreading limb, usually large and showy, 1-1.5 cm. long (or smaller in depauperate specimens), the lobes rounded about 2 mm. long; corolla-scales 2 mm. long, 0.5 mm. wide, semi-elliptic-ovate, attached to the base of the filaments; stamens 4.5-6 mm. long, the filaments hairy near the base, the anthers about 0.66 mm. long; style and branches 5 mm. long, the branches 0.5-1 mm. long, the style hirsutulous near base; ovary 1 mm. long, hirsutulous, ovules 36-43; capsule 3-4 mm. long, oblongish, truncate obtuse and apiculate; seeds 0.5 mm. long, elliptic, subquadrangular, truncate at ends, coarsely pitted, black-brown.

Only three collections have been seen that are referable to typical *P. glechomifolia*: the type, collected "between Peach Springs and the Grand Canyon" by Asa Gray in 1885 (G); parts of a robust plant from the "Grand Canyon" collected by Mr. and Mrs. J. G. Lemmon in 1884 (US); and a plant from "Arizona" collected by Dr. E. S. Clark in 1886 (Herb. Brandegee, Univ. Calif.). In all of these, the plants are robust for the *P. pulchella* relationship and are marked by excellent and distinctive characters. It is remarkable that typical plants were found in a period of only three years and have not been seen since then. These collections were made before the road between Williams and El Tovar was opened, at a time when visitors to the canyon probably went from the railroad by the shortest route, which was north from Peach Springs. It may be that the typical form of *P. glechomifolia* will be found only in a restricted district in that part of Mohave Co., Arizona, between Peach Springs and the Grand Canyon, where Gray collected the type and where the Lemmons collected so assiduously in 1884 (cf. type localities of *Phacelia Lemmonii* Gray and *P. saxicola* Gray).

Several other collections of less robust plants seem referable to *P. glechomifolia*: Havasupai Canyon, Coconino Co., Whiting No. 1047 (Sac), Clover No. 6324 (CAS) and Clover No. 6407 (CAS, P); lower end of Toroweap Valley at 4200 ft., Mohave Co., Alexander in 1933 (UC); Lake Mead,

Mohave Co., *Clover No. 6069* (CAS). These come from localities on either side of the Colorado River Canyon to the east and west of the Peach Springs district. In appearance these specimens are intermediate between typical *P. glechomifolia* and certain aspects of *P. filiformis* which is found in the Canyon still farther east, but *P. glechomifolia* is to be distinguished by the somewhat larger lavender flowers and more numerous seeds.

Phacelia pulchella var. *Gooddingii* has been found in the same region and intermediates between it and *P. glechomifolia* have been studied (cf. *Peebles No. 15007* from Havasu Canyon, described under *P. pulchella* var. *Gooddingii*). This series of plants from *P. pulchella* var. *Gooddingii* and *P. glechomifolia* on the west to *P. filiformis* on the east is an excellent example of the genetic differentiation and segregation that has followed geographic lines discussed under *P. pulchella*.

7. *PHACELIA FILIFORMIS* Brand, Beil. Jahresb. Kgl. Gymnas. Sorau, 8 (1911)

Weak and slender plants of shaded ledges or sturdier few-branched erect or spreading plants of more open exposed places, annuals, 0.5-3 dm. tall, stems glandular-puberulent; leaves chiefly cauline, ovate and elliptic to round, 0.5-3 cm. long and wide, subentire to saliently repand-dentate with rounded lobes, finely and sparsely hirsutulous and glandular, apex obtuse, base rounded, truncate or cordate, petioles 0.5-5.5 cm. long; racemes laxly few- to many-flowered, peduncled, very short to 2 dm. long, pedicels 0.5-1.5 cm. long; sepals in flower oblanceolate or spatulate-oblanceolate, 2.5-3.5 mm. long, 0.5-1 mm. wide, in fruit linear-oblong to oblong-spatulate, 5-6 mm. long, 0.66-1.5 mm. wide, glandular and finely hirsutulous; corollas campanulate-funnelform with rather open tubular yellowish throat and spreading white or lavender limb, 5-8 mm. long and about as wide, the lobes rounded, 1.5-2.5 mm. long; corolla-scales rather conspicuous, semi-oblanceolate to semi-oval, 2 mm. long, 0.3-0.5 mm. wide; stamens unequal, 3.5-5 mm. long, filaments sparsely long-hairy near base, anthers 0.5-0.66 mm. long; style and branches 2.5-5 mm. long, branches 0.3-0.5 mm. long, style sparsely hairy; ovary 1 mm. long, sparsely hirsutulous and glandular, ovules 20-24; capsules 3-5 mm. long, broadly oblongish or elliptical, truncately obtuse and apiculate; seeds plumply oblong, 0.66-1 mm. long, rounded at ends, shallowly and coarsely pitted, brown.

Known only from the Grand Canyon, Coconino Co., Arizona, most of the collections being made between May 1 and July 15.

Collections: Grand Canyon, 7000 ft., *MacDougal No. 186* (UC, type; Ariz, CAS, G. NY, RM, US); Hermit Trail under cliffs, *Eastwood No. 5667* (CAS, G, IU, P, Sac, US); Hermit Trail (probably on open slope), *Eastwood No. 5824* (CAS); Grand View Trail, *Eastwood No. 5751* (CAS, P), *Thorner No. 8471* (Ariz); Bright Angel Trail at 3100 ft., *H. & V. Bailey No. 1082* (CAS), at 6000 ft., *G. B. Grant No. 5722* (DS); Cliff Spring, 1 mile from Cape Royal on North Rim, 7500 ft., *Peirson No. 7425* (CAS, FP); Cape Royal under ledges, *Eastwood & Howell No. 945* (CAS, G).

Phacelia filiformis, as it is accepted here, presents two distinct aspects which are believed to represent different responses of the species to the imme-

diat environment, depending on whether the plants grow in the perpetual shade and suffused light of shelving ledges or in the bright sun of open exposed slopes. The shade-form is the one originally described by Brand and in it the limb of the corolla is white. In appearance the sun-form approaches slender less robust forms of *P. glechomifolia*, but in *P. filiformis* the corolla is usually smaller and the number of seeds is only about half as many.

8. PHACELIA LEMMONII Gray, Synop. Fl. N. Amer. ed. 2, 2(1):417 (1886)

P. heterosperma Parish, Bot. Gaz. 13:37 (1888).

P. polysperma Brand in Engler, Das Pflanzenr. IV. 251: 119 (1913).

Plants annual, finely glandular-puberulent, hirsutulous hairs lacking on the stems, generally 1-2 dm. tall, in depauperate specimens as low as 0.5 dm., in robust specimens as tall as 4 dm., erect, usually substrictly so, or sometimes with the lowest branches more or less spreading or even divaricate, leafy throughout and branching mostly above the base; leaves oblong or elliptical to broadly ovate or suborbicular, generally 1-2.5 cm. long, 0.5-2 cm. wide, finely glandular-puberulent and hirsutulous or scabridulous, obtuse or acute, at the base mostly cuneate or sometimes truncate or subcordate, subentire and repand to prominently crenate or dentate-lobed, petioles mostly less than 1 cm. long; racemes shortly stalked or sessile, generally 1-2.5 dm. long, the lower flowers distant, the upper more crowded; sepals in flower 2.5-4 mm. long, 0.33-1 mm. wide, oblong or oblong-oblancoelate, glandular and hirsutulous, in fruit 5-7 mm. long, 0.5-2 mm. wide, unequal, oblancoelate or oblancoelate-spatulate; corolla tubular-campanulate, 4-6 mm. long, 3-4 mm. wide, white to pale violet; scales free from the filaments, variable even in 1 flower, semi-linear-oblancoelate to semi-oval, 1-1.5 mm. long, or even almost obsolete; stamens 2-3 mm. long, filaments glabrous, anthers 0.25-0.33 mm. long; style including branches 2-2.5 mm. long, the branches 0.5 mm. long, the style glabrous except for a few hairs and glands at very base, ovary 1 mm. long, ovules 70-140, generally about 100; capsules oblong or elliptical, 3-4 mm. long, glandular-puberulent or hirsutulous, obtuse or acutish, apiculate; seeds plumply oblong or ovate to almost round, 0.5 mm. long or a little less, coarsely few-pitted, dark brown.

Desert mountains 3000 to 7000 ft., southern and southeastern California north to middle western Nevada and east to central Arizona. March-July.

Collections. California: Grapevine Canyon at south end of Saline Valley, 4500 ft., Inyo Co., Kerr in 1937 (CAS); Emigrant Canyon, Panamint Mts., 4500 ft., Inyo Co., Gilman No. 2187 (P); Argus Mts., Inyo Co., Purpus No. 5445 (G, M, UC); Old Dad Mts., San Bernardino Co., M. E. Jones No. 25567 (CAS, DS, M, P); Providence Mts., San Bernardino Co., Hoffmann in 1930 (CAS); north slope of San Bernardino Mts., 4000-6000 ft., San Bernardino Co., Parish No. 3792 (G, ND, UC); Rock Creek, Los Angeles Co., Parish No. 1980 (DS, type of *P. heterosperma* Parish; CAS, F, G, NY, UC); Rock Creek, 3800 ft., Los Angeles Co., Abrams & McGregor No. 560 (US, type of *P. polysperma* Brand; DS, NY); Shumway, Santa Rosa Mts., 4000 ft., Riverside Co., Munz No. 15101 (CAS, M, P, RM, UC). Nevada: 1 mile NW of Burnt Cabin Summit, 6400 ft., SE, Churchill Co., Beach No. 1001 (UC); Nixon Peak, Kawich Range, 6900 ft., Nye Co., Ripley & Barneby No. 3736

(CAS, FP); Eldorado Canyon at Nelson, 3000 ft., Nye Co., *M. E. Jones in 1907* (DS, P). Arizona: Mineral Park, Mohave Co., *Lemmon No. 3350* (G, type of *P. Lemmonii* Gray); Truxton Canyon, Mohave Co., *Mr. & Mrs. Lemmon No. 3350* (UC); between Peach Spring and Kingman, Mohave Co., *N. C. Wilson in 1893* (ND); Castle Creek, Yavapai Co., *Townley No. 4978* (Ariz.).

Although *P. Lemmonii* is a widespread species in the desert ranges of southwestern America, it is not a common plant. It grows in moist places and in wet sand along streams, in this regard quite different from its relative, *P. Parishii* Gray, which is found on arid alkaline flats or alluvial slopes.

The species presents a rather uniform appearance throughout its range, the most distinctive collections being those by Lemmon from Mohave County, Arizona. In them the lowest branches are more divaricate or rather widely ascending, while in the more widespread form of plant the stems are substrictly erect. Further field work in northwestern Arizona may indicate that these variants should receive taxonomic recognition.

9. PHACELIA PARISHII Gray, Proc. Amer. Acad. 19:88 (1883)

P. salina M. E. Jones in Brand, Das Pflanzenr. IV. 251:119 (1913), as synonym.

Plant annual, the stems branching widely from the base, spreading and ascending, 5-15 cm. long, finely glandular-puberulent; leaves oblongish or elliptic to ovate or obovate, 1-3 cm. long, 0.5-2 cm. wide, or in depauperate specimens smaller, sparsely glandular and scabridulous, obtuse, cuneate at base, margin somewhat revolute, entire or undulate to crenate-dentate, petioles 1-2 cm. long below, almost none above; racemes rather densely flowered, borne on generally elongate stems above the leafy part of the plant, pedicels 0.5-2 mm. long; sepals in flower 3.5-4.5 mm. long, very unequal in width, 1-2.5 mm. wide, linear-oblong to obovate, glandular-puberulent and hirsutulous, in fruit much enlarged, 6-7.5 mm. long, four of the sepals oblanceolate and 1.5-2.5 mm. wide, the fifth sepal obovate-spatulate and 2.5-4 mm. wide; corolla tubular-campanulate, 5-6 mm. long, the limb and upper part of the tube lavender, the lower part of tube pale yellowish; scales small, about 1 mm. long, semi-oval or variable in shape; stamens 2.5-3.5 mm. long, filaments sparsely hairy at base, anthers 0.5 mm. long; style and branches 1.5-2 mm. long, the branches 0.5 mm. long; ovary 1-1.25 mm. long, sparsely hairy or hirsutulous, ovules 30-43; capsules ovate-oblong, 4 mm. long; seeds oblong, 1-1.3 mm. long, black or brown, obtuse or subacute at ends, finely pitted.

Occasional in desert valleys on alkaline flats and alluvial slopes, California and Nevada, 2000 to 6000 ft. April-July.

Collections. California: dry alkaline lake near Rabbit Springs, San Bernardino Co., *S. B. & W. F. Parish No. 1314* (G, type; DS, F, NY, UC, US); Lucerne Dry Lake below Rabbit Springs, *Ripley & Barneby No. 3265* (CAS, P). Nevada: alluvial flats near Las Vegas, Clark Co., *Eastwood & Howell No. 8958* (CAS, G, IU, P, RM, US); arid gravelly slopes, south base of Pintwater Mts., Clark Co., *Barneby No. 2917* (CAS); lake-bed between Spotted and Pintwater ranges, Clark Co., *Barneby No. 2912* (CAS); foothills of Spotted Range towards Frenchman Flat, Nye Co., *Ripley & Barneby No. 3425* (CAS, FP); Muncy, White Pine Co., *M. E. Jones in 1906* (DS, P); Steptoe Valley, White Pine Co., *M. E. Jones in 1891* (CAS, G, P, UC, US).

The unequal development of the fruiting sepals is a mark by which *P. Parishii* may be distinguished from its relatives. The low spreading plants have a distinctive appearance which is also shared by members of the *P. pulchella* group, but in regions where their ranges overlap, the latter have much showier corollas.

10. *PHACELIA SAXICOLA* Gray, Proc. Amer. Acad. 20:169 (1884)

Plant annual, the stems branching from the base, erect or spreading, 2-12 cm. tall and sometimes about as broad, with shorter capitate-glandular hairs and longer scattered hirsute hairs; leaves oblanceolate-spatulate, oblong and elliptic or rarely ovate, 5-7 mm. long, 2-4 mm. wide, entire, obtuse, long-attenuate at base into a slender petiole up to 7 mm. long, the uppermost leaves very much reduced, the blades glandular and hirsute, the nonglandular hairs becoming white-crustaceous; racemes elongate and loosely flowered, shortly peduncled, pedicels 1-3 mm. long; sepals in flower 3.5-4 mm. long, 0.5 mm. wide, linear-oblong to linear-oblanceolate, glandular and hirsutulous, in fruit 5-7 mm. long, 0.5-1.5 mm. wide, oblanceolate-spatulate, the segments united at base nearly 1 mm.; corolla tubular, 3-4 mm. long, the limb lavender-blue, the tube white, the outside of the lobes and upper part of throat glandular and hirsutulous, corolla not readily deciduous, splitting from base upward over the expanding capsule; corolla-scales 0.5-0.75 mm. long, linear; stamens 1.3-2 mm. long, the filaments glabrous or with few hairs, anthers 0.25 mm. long; style and branches 1.5 mm. long the branches less than 0.5 mm. long; ovary about 1 mm. long, bristly-hairy, ovules about 60; capsule rotund-oblong, 2.5 mm. long, nearly 2 mm. wide, truncate but apiculate; seeds roundish, 0.3-0.4 mm. long, blackish, shallowly and rather broadly reticulate-pitted or nearly smooth.

A rare plant of desert mountains and high plateaus from eastern California east to southern Nevada and northern Arizona, 3000 to 7000 ft. April-September.

Collections. California: Sherwin Grade 6200 ft., Mono Co., *Peirson No. 12418* (CAS, FP, NY); Tafel Canyon, 17 miles N. of Darwin, Inyo Co., *Jaeger in 1938* (P); calcareous rocks, Grapevine Canyon, 3400 ft., Inyo Co., *Ripley & Barneby No. 3683* (CAS). Nevada: Pahroc Spring, Lincoln Co., *Purpus No. 6303* (UC, US). Arizona: Kingman's Station, Mohave Co., *Lemmon in 1884* (G, type); 1 mile east of Kingman, *Ripley & Barneby No. 3385* (CAS, DS); near El Tovar, Coconino Co., *Eastwood No. 3794* (CAS); Cliff Dwellings, Grand Canyon, Coconino Co., *Eastwood No. 5784* (Ariz. CAS, P). It would seem that the original collection was distributed with varying data. The label on the type sheet gives Kingman's Station, April 26, 1884, *Lemmon*. A printed label in Herb. U. C. and Herb. U. S. reads: "Kingman, on granite rocks, and Peach Springs. Coll. by J. G. Lemmon and wife." In Herb. Brandegee. (UC) a specimen is labelled in Lemmon's hand: "Near Kingman Station, N. Ariz. Also at Peach Spring, May 10th, '84."

Although *P. saxicola* has all of the characters used to indicate the desert species being treated in this study, it is to be distinguished by two remarkable characters which mark it as different from most species in *Phacelia*. The most notable is the marcescent character of the corollas, which, if not permanently

persistent, are only tardily forced from the plant by the fruiting capsule. This character of the corolla, which is one of the chief marks of the hydrophyllaceous genera *Emmenanthe* and *Miltitzia*, is shared by a few species of *Phacelia*, such as *P. sericea* (Grah.) Gray and relatives in the subgenus *Eutoca* and by *P. marcescens* Eastw. in *Euphacelia*.

Another distinctive character of *P. saxicola* is the peculiar marking of the seed-coat. In all the other species included in this study, the seeds are distinctly and often coarsely and deeply pitted or foveolate, but in *P. saxicola* the seed-coat is shallowly reticulate-pitted at most, and more often it is nearly smooth with only the faintest suggestion of reticulations.

The immediate affinities of *P. saxicola* are not apparent though perhaps it is as closely related to *P. incana* Brand as to any other species. It is frequently, though not exclusively, found on calcareous substrata. According to data accompanying Ripley and Barneby's collection from the type locality, the plants grew in "fissures of exposed dome-like calcareous rocks" and not "on granite rocks" as Lemmon thought.

11. PHACELIA BARNEYANA J. T. Howell, Leaf. West. Bot. 3:191 (1942)

Plant annual, 0.4-1.5 dm. tall, slender and erect, purplish-tinged, simple or few-branched mostly near the base, the stems hirsutulous-villous, the longer straight spreading hairs capitate-glandular, the shorter finer spreading hairs non-glandular; leaves mostly on the lower part of the stems, elliptic-oblong to ovate, 0.4-1.5 cm. long, 0.2-0.7 cm. wide, entire or somewhat repand or serrate with 1 to 3 rather prominent serrations on each side, hirsutulous and glandular, obtuse or subacute, broadly cuneate to rounded at base, petioles to 2 cm. long; racemes substrict, elongate, to 1 dm. long, the flowers distant, pedicels slender, 0.4-1 cm. long, spreading or ascending, longer than the calyx in fruit; calyx-segments in flower 2-2.5 mm. long, linear-oblong to oblanceolate, in fruit 3-4 (or 4.5) mm. long, sparsely hirsutulous and glandular, scarcely exceeding the capsule; corolla very pale lavender, tubular-campanulate (3-) 4.5-5 mm. long, glabrous outside, the lobes 0.6-1 mm. long; corolla-scales linear or reduced to a line bearing one or two hairs or obsolete; stamens nearly equal, 2 mm. long, inserted rather high in tube of corolla, filaments glabrous, anthers roundish, 0.25-0.33 mm. in diameter; style 2 mm. long, glabrous, the branches very short and capitate, about 0.2-0.3 mm. long; ovary 0.75 mm. long, long-hirsutulous above, pubescent below, ovules 18-20; capsule 3-4 mm. long, elliptic-oblong to broadly ovate, rounded and shortly apiculate, sparsely hirsute with long hairs; seeds plumply ovatis, 0.75-1 mm. long, brown or blackish, coarsely pitted.

Collections, all from California: Clark Mt. near Mountain Pass, 5500 ft., eastern San Bernardino Co., May 8, 1941, Ripley & Barneby No. 3362 (type, CAS); head of Johnson Canyon, 8000 ft., Panamint Mts., Inyo Co., Gilman No. 3134, June 16, 1938 (P); and, south of Seep Hole Spring, east side of Inyo Mts. near summit, Inyo Co., Kerr No. 3271, July 3, 1941 (CAS, DS, F, G, US). Concerning the occurrence of his elegant little *Phacelia*, Mr. Barneby has written as follows: "It was very scarce, only about twelve plants seen in a single patch in rather rich loose gravelly (calcareous)

soil with some humus around a juniper, but mostly in the open. It grew with *P. coerulea* Greene, *P. affinis* Gray, and *Antirrhinum Kingii* Wats. The corolla is very pale but quite conspicuous, the purple coloring being much accentuated in drying."

Phacelia Barnebyana is related to both *P. incana* Brand and *P. nevadensis* J. T. Howell (*P. pusilla* Torr., not Buckl.) but from both of them it differs in its more slender habit, purple-tinged stem, more glandular indument, frequently toothed leaves, and much smaller calyces. It resembles *P. nevadensis* in having the leaves predominantly near the base of the plant and in having slender elongate pedicels longer than the fruiting calyces, but with its almost strictly erect stems and inflorescences, it does not look at all like that rare and little-known species. *Phacelia Barnebyana* might be mistaken for a depauperate form of *P. rotundifolia* but it does not seem to be so closely related to that species from which it may be readily distinguished by its slender elongate pedicels and differently shaped leaves.

12. PHACELIA NEVADENSIS J. T. Howell, Leaf. West. Bot. 3:120 (1942)

P. pusilla Torr. ex Wats., Bot. U. S. Geol. Explor. 40th Paral. (King's Exped.) 253 (1871), not *P. pusilla* Buckl., Amer. Journ. Sci. 45: 172 (1843).

Plant annual, 8 cm. tall, slender and erect, branching near the base and the branches divaricately spreading, the stem finely glandular-villous, the glands capitate on slender stalks, the non-glandular pubescence shorter and finely hirsutulous; leaves broadly ovate or elliptical, about 1 cm. long, 0.6-0.8 cm. wide, glandular and hirsutulous, entire, obtuse or acute, at base cuneate or subtruncate, petiole slender, as long as the blade; racemes loosely flowered, the lowest flowers on long slender pedicels 1-1.5 cm. long, much longer than the calyx in fruit, the upper pedicels shorter, 2-5 mm. long, erect or spreading; sepals in flower 3-3.5 (or nearly 4) mm. long, linear or linear-oblong, glandular and hirsutulous, in fruit 7 mm. long, linear-oblong, rather sparsely glandular-hirsutulous, spreading a little at the tip; corolla tubular-campanulate, hairy outside, 4.5 mm. long, the lobes 1 mm. long; corolla scales "narrow"; stamens nearly equal, the anthers roundish, 0.2 mm. long; style 1.5 mm. long, the branches very short, about 0.2 mm. long, capitate, the style hirsutulous to the middle; capsule 4.5-5 mm. long, oblong-ovate, sparsely hirsutulous, obtuse or subacute, apiculate; seeds about 20 ("18-24"), a little over 1 mm. long, ovate, acutish at one end, subtruncate at other end, coarsely pitted, brown.

Phacelia nevadensis is known only from the single collection made by Watson in the East Humboldt Mts., 6500 ft., Elko Co., Nevada, in July, 1867 (G, type; US). It is closely related to *P. incana* Brand but is a more slender plant with all parts of the flower and fruit somewhat larger than in *P. incana*. When Torrey originally described *P. pusilla*, he cited with the type a plant collected by Watson under the same number at Steamboat Springs in western Nevada. Although this plant subsequently served as the type of *Emmenanthe pusilla* Gray (Proc. Amer. Acad. 11:87, 1876), Brand cited the collection as *P. pusilla* Torr. (1913, p. 122). In Herb. N.Y. Bot. Gard.,

there is a specimen of the Steamboat Springs plant but *P. pusilla* is represented only by the set of Torrey's drawings.

13. *PHACELIA INCANA* Brand, Beil. Jahresb. Kgl. Gymnas. Sorau, 8 (1911)

Plants annual, 0.5-1.5 dm. tall, substrictly erect, branching from the base and above, the stems glandular-villous with soft spreading hairs; leaves elliptic-oblong to ovate, 0.5-1.5 cm. long, 0.3-1 cm. wide, obtuse or subacute, rounded or truncate at base, sometimes asymmetric, entire, villous with hirsutulous non-glandular hairs and short capitate glandular hairs, petioles quite villous, 0.3-2 cm. long; racemes elongate, to 9 cm. long, laxly flowered, generally sessile, pedicels shorter than the fruiting calyx, 1-5 (or rarely 7) mm. long; sepals in flower 3-3.5 mm. long, hirsute and capitate-glandular, linear-oblancoolate to oblong, in fruit mostly 4.5-6 (or rarely 7) mm. long, linear-oblancoolate, spatulate, spreading a little at the tip; corolla 3.5-4 mm. long, tubular-campanulate, white or lavender-tinged above, pale yellowish below, the lobes 1 mm. long; corolla-scales 1-1.25 mm. long, narrow but gradually widened upward; stamens nearly equal, 2.5-3 mm. long, filaments sparsely hairy near base, anthers 0.25-0.33 mm. long; style 1.5 mm. long the branches very short, 0.2-0.25 mm. long or rarely longer, hirsutulous nearly to the branches; ovary hairy, about 0.75 mm. long, ovules 23-37; capsule 3.5-4 mm. long oblong or ovate-oblong, 3.5-4 mm. long; seeds elliptic or ovate, 0.6-1 mm. long, acutish or obtuse at ends, rather coarsely pitted, brown.

Calcareous slopes of desert mountains from central Idaho and Wyoming south to western Utah and eastern Nevada, 5000 to 7000 ft. May-July.

Collections. Idaho: limestone knolls, Mountain Pass, 7 miles north of Dickey, 6500 ft., Custer Co., *Hitchcock et al. No. 3772* (CAS, DS, IU, RM, UC). Wyoming: Solon, *Williams in 1897* (NY). Nevada: Currie, Elko Co., *M. E. Jones in 1906* (P); calcareous gravel, Pequop Mts., Elko Co., 6300 ft., *Ripley & Barneby No. 4605* (CAS); Pilot Peak south of Montello, 4700 ft., Elko Co., *Ripley & Barneby No. 4617* (CAS); Glencoe, White Pine Co., *M. E. Jones in 1891* (P); under junipers on calcareous slopes, Highland Range west of Caliente, Lincoln Co., *Ripley & Barneby No. 3508* (CAS). Utah: Dugway, May 28, 1891, *M. E. Jones* (UC, type; CAS, DS, M, NY, P, RM, US); Dutch Mt., Tooele Co., *M. E. Jones in 1891* (P); Detroit, Millard Co., *Jones in 1891* (P); calcareous slopes, 2 miles south of Garrison, Millard Co., *Ripley & Barneby No. 3571* (CAS).

Dugway, the type locality, has not been found on any map that I have examined. From the manuscript journal of collecting trips of Marcus E. Jones (1937, p. 19), we learn that on May 28, 29, and 30, 1891, he was "at Dugway which is on the north end" of the Dugway Range. Presumably this is the Dugway Range of present maps, and if so, it would place Dugway in Tooele County, Utah. On some specimens, the date of this collection is given as July 13, 1891; but at that time, according to his journal, Jones was in White Pine County, Nevada. Certainly, in 1891, Jones made the finest series of specimens that has yet been obtained in *P. incana*. Of the fifteen collections of this species that I have examined, eight were collected by him in 1891 in the Basin ranges of middle western Utah and adjacent Nevada.

14. *PHACELIA PEIRSONIANA* J. T. Howell, Leaflet. West. Bot. 3:117 (1942)

Plants annual, glandular-villous or glandular-puberulent, few hairs hirsutulous and non-glandular, 1-4 dm. tall, erect, leafy throughout and branching above and with few ascending branches from the base; leaves broadly ovate to orbicular or even broader than long, mostly 1-3.5 cm. long and wide, obtuse, cordate or reniform to truncate or even rounded at base, glandular and scabrid-hirsutulous, dentate-crenate, or more generally repand-crenate, petioles 1-4 (or 6) cm. long; raceme sessile or shortly peduncled, loosely flowered, the lowest flowers distant from each other, more closely flowered above, pedicels mostly 1-5 mm. long, rarely the lowest 10 mm. or more long; sepals in flower 3-4 mm. long, 0.5-0.75 mm. wide, linear-oblong or oblanceolate-oblong, strongly accrescent in fruit, becoming 7-8 mm. long, 1-3 mm. wide; corolla tubular-campanulate, mauve or white, 5 mm. long, 3.5-4 mm. across, the lobes scarcely spreading, 1-1.5 mm. long; corolla-scales variable, narrow and oblongish or wider and semi-oval or semi-obovate, 1-1.5 mm. long, free from the filaments; stamens a little unequal, 2.5-3.3 mm. long, the filaments sparsely hairy at base, the anthers tiny, 0.3-0.5 mm. long; style including branches 2-3 mm. long, branches short, 0.25-0.5 mm. long; ovary 1 mm. long, hirsutulous, ovules 40-50; capsule 4-6 mm. long, oblong, obtusely truncate, apiculate; seeds brown or black, oblongish, 1-1.3 mm. long.

Desert mountains from eastern California south and east to southern Nevada, 4500 to 8000 ft. May-August.

Collections. California: crevices of volcanic rock west of Little Round Valley, 7000 ft., Mono Co., J. T. Howell No. 14353 (CAS, type; Ariz. DS, F, FP, G, IU, M, ND, NY, P, RM, UC, US); summit of Sherwin Hill, 6400 ft., Mono Co., Peirson No. 11161 (CAS, FP); Westgard Pass road, 6500 ft., Inyo Co., Keck No. 536 (CAS, DS, P). Nevada: Big Indian Canyon, Hawthorne, 5000 ft., Mineral Co., M. E. Jones in 1897 (P); summit of Gold Mt., 8000 ft., Esmeralda Co., Keck No. 575 (CAS, DS); calcareous gravel under cliffs, Muddy River Valley, 2 to 3 miles south of Caliente, 4500 ft., Lincoln Co., Ripley & Barneby No. 3514 (CAS, G).

As in the case of other round-leaved species in this group, *P. Peirsoniana* has generally been called *P. rotundifolia* in collections, although it is not so nearly related to that species as to *P. mustelina* Cov. Superficially it may be confused with certain aspects of *P. Lemmonii* Gray but an obvious difference between that species and *P. Peirsoniana* is that the petioles of the lowest leaves of *P. Lemmonii* are shorter than the blades while in *P. Peirsoniana* they are longer.

15. *PHACELIA ROTUNDIFOLIA* Torr. ex Wats., Bot. U.S. Geol. Explor.
40th Paral. (King's Exped.) 253 (1871)

Plants annual, hirsute and glandular, 0.3-3 dm. tall and generally about as broad, the stems erect and fastigiately few-branched or the lowest branches more widely spreading with ascending branchlets; leaves roundish, mostly 0.5-2 cm. in diameter, rounded to broadly cordate or reniform at base, coarsely and radiately toothed, the teeth rather few and sometimes lobe-like, petioles

to 3.5 cm. long; racemes elongate and rather loosely flowered, to 2 dm. long with short (0.5-1.5 cm.) peduncles, pedicels mostly 1-5 mm. long; sepals in flower 2-4 mm. long, linear-oblongate, in fruit 5-6 mm. long, to 1 mm. wide, somewhat unequal, spatulate, bristly-hirsute and glandular; corolla tubular, about 5 mm. long and 2.5 mm. wide, white or very pale mauve above, pale yellow below; corolla-scales small, 0.5-1 mm. long, free from the filaments except at very base; stamens 2-2.5 mm. long, the filaments glabrous, the anthers 0.25-0.33 mm. long; style and branches 1.5-2 mm. long, the branches about 0.5 mm. long, sparsely hairy below the middle; ovary 0.75 mm. long, the ovules 60 to more than 100; capsule 4 mm. long, oblong, minutely puberulent, the compressed apex triangular-acute and beaked; seeds less than 0.5 mm. long, rotund-oblong, rounded at ends, brownish, rather coarsely pitted.

Desert mountains, 300 to 6000 ft., from southeastern California east to southwestern Utah and south to western Arizona. April-June.

Collections, California: rocky wash, west side of Westgard Pass, Inyo Co., *Eastwood & Howell No. 9597* (Ariz. CAS, F); crevices of limestone rocks, Mazurka Canyon, Inyo Mts., 6000 ft., Inyo Co., *Kerr No. 660* (CAS); 2 miles east of Bradbury Well, Black Mts., Inyo Co., *J. T. Howell No. 3636* (CAS, G, NY); canyon below Aguerberry Point, Panamint Mts., Inyo Co., *Eastwood & Howell No. 7840* (CAS); above Vontrigger Spring, eastern Mohave Desert, 3500 ft., *Munz No. 13673* (DS, P, UC); Needles, San Bernardino Co., *M. E. Jones in 1884* (G, P); Copper Creek Basin, Whipple Mts., *Peirson No. 11485* (CAS, FP, G, P); Cushenberry Canyon at 4500 ft., San Bernardino Co., *Parish No. 3607* (DS), at 4200 ft., *Munz No. 10942* (P); east of Palm Springs, 1000 ft., Riverside Co., *Peirson No. 4125* (FP). Nevada: Amargosa Desert, 4000 ft., Nye Co., *M. E. Jones in 1907* (DS, P); Caliente, 4400 ft., Lincoln Co., *M. E. Jones in 1904* (P); limestone ridge southwest of Crystal, Clark Co., *Eastwood & Howell No. 8986* (CAS, DS, F, P, UC); Kyle Canyon, Charleston Mts., Clark Co., *Clokey No. 7647* (CAS, DS, IU, NY, US). Utah: type collection *Palmer in 1870* (NY, type; G, US); St. George, Washington Co., *Parry No. 183* (DS, F, G, M, US), *Palmer No. 338 in 1877* (NY, US), *M. E. Jones No. 2029* (F, IU, P, US); 1 mile east of Hurricane, 3400 ft., Washington Co., *Maguire & Blood No. 1506* (IU, M, RM, UC). Arizona: on calcareous rocks, 2 mile northeast of Kingman, Mohave Co., *Ripley & Barneby No. 3384* (CAS); Yucca, Mohave Co., *M. E. Jones No. 3914* (Ariz. CAS, DS, F, G, IU, NY, P, RM, UC, US); Sheep Tanks, Yuma Co., *Kearney & Peebles No. 11018* (Sac, US); Bright Angel Trail, Grand Canyon, 3100 ft., Coconino Co., *H. & V. Bailey No. 1083* (CAS).

Phacelia rotundifolia is the most common and widespread species in the group being treated in this paper and it is also the most abundantly collected. Although its distribution partakes of the insular type of distribution characteristic of these desert species, there are no outstanding variants to be noted since the species is nearly uniform throughout its range.

16. PHACELIA MUSTELINA Cov., Journ. Wash. Acad. Sci. 27:196 (1937)

Plants annual, glandular-villous and more or less hirsutulous, mostly 1-3 dm. tall, or in depauperate specimens blooming when only 3 cm. tall, simple at base and branching above or widely branching from the base; plant leafy throughout, leaves oblong-ovate to orbicular, 0.5-3.5 cm. long, 0.2-3 cm. wide, obtuse, generally cordate or subcordate, rarely truncate and abruptly cuneate, margin prominently and somewhat irregularly crenate or dentate, rarely sub-

entire, petiole 0.3-4 cm. long; racemes rather loosely flowered and elongate (except in depauperate specimens), to 1 dm. long on peduncles to 4 cm. long, pedicels 1-6 mm. long, more or less spreading; sepals in flower 3-4.5 mm. long, oblanceolate, in fruit not much accrescent, becoming 4-5.5 mm. long; corolla tubular-campanulate, violet, 6-10 mm. long, 4-8 mm. across; corolla-scales 1-3.5 mm. long, diverse even in one flower, usually attached to the base of the filaments for some distance; stamens more or less unequal, 3-5 (or 8) mm. long, filaments sparsely short-hairy, anthers 0.5-0.66 mm. long; style including branches 3-4 (or 7) mm. long, the branches 0.5-1 mm. long; ovary 1-1.5 mm. long, the numbers of ovules variable, (28-) 40-70 (-80); capsules 4 mm. long, oblong, obtuse, mucronate; seeds rotund-oblong, dark brown or dull brown, coarsely pitted, 0.5-0.66 mm. long.

A rare plant known from the mountains bordering Death Valley, California, and from adjacent Nevada in the Skull Mts., 3000 to 6000 ft. March-June.

Collections. California: head of Titus Canyon, Grapevine Mts., Inyo Co., Gilman No. 1810 (US, type); Titus Canyon, Eastwood & Howell No. 7777 (CAS), Munz No. 16415 (P); Wood Canyon, Panamint Mts., Inyo Co., Gilman No. 1751 (P); Emigrant Canyon, Panamint Mts., Inyo Co., Gilman No. 2187a (P); Grapevine Canyon above Scotty's, Inyo Co., Ripley & Barneby No. 3681 (CAS, G); Granite Wells, San Bernardino Co., Peirson No. 2650 (CAS, FP). Nevada: north end of Skull Mts., Nye Co., Ripley & Barneby No. 3436 (CAS).

The collections of *P. mustelina* that have been available for study have shown it to be diverse both in appearance and in morphological characters. Unfortunately the type is a fragmentary specimen of a young plant but it seems to be less like the much-branched collections cited above from Titus Canyon, the type locality, than the other specimens that are listed. The variant which is most diverse is a robust plant collected in Dante's Canyon, Black Mts., Inyo Co., on Nov. 6, 1938, by M. French Gilman, No. 3499 (P, frag. CAS), in which the size of the flower-parts is considerably more than in other collections but in which the number of ovules (perhaps due to the lateness of the season) is much-reduced. Genetically considered, this plant probably bears the same relation to the rest of *P. mustelina* that the "giant" form of *P. pulchella* var. *Goodingii* from near Crystal, Nevada, bears to the rest of that entity.

17. PHACELIA GERANIIFOLIA Brand, Beil. Jahresb. Kgl. Gymnas.
Sorau, 7 (1911)

P. perityloides Cov. var. *Jaegeri* Munz, Man. S. Calif. Bot. 412, 600 (1935).

Plant perennial, the caudex crowned by a thick cushion of many abbreviated densely leafy stems from among which several elongate more sparsely leafy stems of the season arise, these latter 0.7-1.5 dm. tall, erect, unbranched, glandular-villous and with scattered, nonglandular, hispidulous hairs, especially below; leaves of abbreviated stems elliptical to ovate or roundish, 2-5 mm. long, subentire or crenate to palmately crenate-lobed, petioles long and slender, 0.5-1 cm. long, the blade and petiole villous and somewhat glandular; leaves

of elongate stems roundish, 0.5-1.5 cm. in diameter, more or less deeply palmately or radiately lobed or toothed, villous-hirsutulous and glandular, base truncate or cordate, petioles 1-2.5 cm. long; racemes laxly few-flowered, flowers 1-5, pedicels 1-3 cm. long, reflexed in fruit; sepals in flower 3.5-4.5 mm. long, 0.5-1 mm. wide, linear-ob lanceolate or oblongish, glandular and hirsutulous, in fruit 4.5 mm. long, 0.66-1 mm. wide, narrowly oblong or oblanceolate; corolla tubular-funnelform, the tube cylindrical, the limb spreading widely, 1.2-1.5 cm. long, 1 cm. across, the limb white, the tube mauve or white; corolla-scales 4 mm. long, linear, widest at the middle, attenuate above into a narrow fold; stamens 4-5.5 mm. long, filaments glabrous, anthers 0.75-1 mm. long; style and branches 4-5.5 mm. long, bristly-hairy up to the branches, branches 0.5 mm. long; ovary 1 mm. long, hirsutulous above, ovules 50-100; capsule oblong-elliptic, 2.5 mm. long; seeds angular oblongish, 0.5-0.75 mm. long and about half as wide, black, truncate or obtuse at ends.

Known only from two localities in southern Nevada and adjacent California.

Collections. Nevada: Sheep Mt., Clark Co., *Purpus* No. 6138 (UC, type; Ariz. NY, P. RM. US); Deadman's Canyon, Hidden Forest, 7000 ft., Sheep Mt., Clark Co., *Alexander & Kellogg* No. 1693 (CAS, UC). California: Clark Mt., eastern San Bernardino Co., *Jaeger* in 1933 (P, type of *P. perityloides* var. *Jaegeri*), in 1930 (P).

The dimorphic stems and the reflexed fruiting pedicels at once distinguished this remarkable plant from its relatives, *P. perityloides* Cov. of California and *P. laxiflora* J. T. Howell of Arizona and adjacent Nevada. According to R. C. Barneby it grows at Sheep Mt. in crevices of limestone cliffs. Notices of the field occurrence of *P. geraniifolia* and *P. perityloides* have recently been published by Dwight Ripley (1942, p. 22) and R. C. Barneby (1942, p. 132).

18. *PHACELIA PERITYLOIDES* Cov., *Proc. Biol. Soc. Wash.* 7:75 (1892)

Plant perennial, the stems loosely spreading or ascending if shorter, 0.5-4 dm. long, the older basal part white-hairy with spreading velutinous-hirsutulous, non-glandular hairs, the pubescence of the stems of the season hirsutulous and glandular; leaves orbicular, mostly 0.5-2 cm. in diameter, coarsely radiate-dentate or shallowly radiate-lobed, hirsute and glandular, truncate or cordate at base, petioles 0.5-3.5 cm. long; racemes laxly few-flowered, 5-10 cm. long, pedicels mostly 0.5-1.5 cm. long; sepals in flower 5 mm. long, 0.75-1.3 mm. wide, oblong to oblanceolate, in fruit slightly enlarged, about 6 mm. long, 1-2 mm. wide, oblanceolate or oblong-oblanceolate, hirsutulous and glandular; corolla tubular-campanulate, 10-11 mm. long, about 7 mm. across, the limb white, the tube yellowish at first, and later becoming purplish; corolla-scales filiform, 2 mm. long; stamens unequal, 3 mm. and 6 mm. long, filaments glabrous, anthers 0.66 mm. long; style and branches 4.25-5 mm. long, the branches 0.2-0.25 mm. long or rarely longer, only the lower part of the style sparsely hairy; ovary 1.25 mm. long, sparsely hirsutulous-hairy, ovules about 200; capsules ovate-oblong, 4 mm. long; seeds oblongish, more or less truncate

at ends and tending to be angular, about 0.5 mm. long, brown, not coarsely pitted.

Known only from the mountains of Inyo County, California, where it is a crevice-plant of canyons or exposed slopes, 2000 to 7500 ft. March-June.

Collections. Johnson Canyon, 5500 ft., Panamint Mts., Coville & Funston No. 524 (type, US); Surprise Canyon, at 4000 ft., J. T. Howell No. 3974 (Ariz, CAS, F, IU, NY), at 5200 ft., Ferris No. 7984 (CAS, DS, F, G, M, P, UC), at 7500 ft., J. T. Howell No. 4014 (CAS, FP, G); Panamint Canyon, M. E. Jones in 1897 (Ariz, DS, G, IU, M, NY, P), Hall & Chandler No. 7025 (G, P, RM, UC, US); Titus Canyon, Grapevine Mts., Peirson No. 11807 (FP), Eastwood & Howell No. 7778 (CAS); Saline Valley, Kerr in 1935 (CAS, P); Black Canyon, White Mts., Duran in 1931 (CAS, UC), Cassel No. 275 (DS).

One of the most remarkable species in a group of distinguished plants, *P. perityloides* is readily recognized by the peculiar hoary velvety pubescence which develops on the older stems of the plant. As in its near relative, *P. laxiflora* J. T. Howell, the sepals become somewhat thickened, and the capsules, which tend to persist on the plants, are chartaceous-hardened.

19. PHACELIA LAXIFLORA J. T. Howell, Leaf. West. Bot. 3:95 (1941)

Perennial with few-branched and more or less trailing stems arising from the crown of a woody root, the stems 1-4.5 dm. long, sordidly glandular-villous; leaves orbicular, 0.5-3.5 cm. in diameter, hirsutulous and glandular, dentate to saliently dentate-lobed, cordate at base, petioles to 3.5 cm. long; racemes laxly flowered with the flowers rather distantly spaced, pedicels mostly 1-3.5 cm. long, becoming thickish in age; sepals in flower 3.5-6 mm. long, oblanceolate, in fruit 5.5-7.5 mm. long, glandular and hirsute, the tips recurved or straight; corolla tubular-campanulate, 13 mm. long, the limb expanded and about 1 cm. across, the lobes rounded, about 3 mm. long, white, the tube pale violet, more or less glandular-pubescent; corolla-scales small, about 1 mm. long, very narrowly semi-lanceolate, reduced above to a line about 1 mm. long; stamens somewhat unequal, 4-5 mm. long, filaments glabrous, anthers 1 mm. long; style and branches 4 mm. long, hirsutulous and glandular, the branches 1 mm. long; ovary 1 mm. long, hirsute above, ovules very numerous, about 220; capsule oblong-ovate, 5.5-6 mm. long, becoming indurate, conspicuously apiculate; seeds oblong, subtruncate at ends, 0.5-0.75 mm. long, shallowly reticulate-foveolate, black and somewhat shiny.

Known only from the region of the Grand Canyon, Mohave and Coconino counties, Arizona, and in the Virgin Mts., Clark Co., Nevada, 2000 to 5500 ft. May-July.

Collections. Arizona: Mohave County: near Toroweap Pt., Hilend (CAS, type): lower end of Toroweap Valley, Alexander in 1933 (UC); Colorado River canyon near head of Lake Mead, Ferris No. 9871 (CAS, DS). Coconino County: Grand Canyon, 4000 ft., MacDougal No. 198 (US); Hermit Trail, Eastwood No. 5823 (CAS); Bright Angel Trail, Thornber No. 8260 (Ariz). Nevada: on limestone, Virgin Mts., 3500 ft., Munz No. 16700 (CAS, P), at 5500 ft., Munz No. 16744 (CAS, P).

Not much is known of environmental conditions at most of the stations

where *P. laxiflora* has been collected. For only two collections, the type and Ferris No. 9871, is the habitat mentioned and both of these describe the plant as growing at springs or in dripping water. This environment is different from that in which the closely related *P. perityloides* Cov. is found, and if it is found to be the usual type with further field work, it will offer a physiological complement to the morphological differences that already separate the species. *Phacelia perityloides* is known to grow only in arid situations on canyon walls and exposed crags, never near springs or seepages.

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A Revision of the *Liatris scariosa* Complex

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The *Liatris scariosa* complex was conservatively treated as one species with one named variety by Asa Gray in the Synoptical Flora, and, at the other extreme, was split into scores of species by E. S. Steele, named on herbarium sheets but never published. The variability of each species in the complex, the occurrence of hybrids, and the scanty representation of some of the species in most herbaria have all contributed to the difficulty of understanding the group. A further contributing factor has been the fact that some of the most obvious variations are of least taxonomic importance. All the species have glabrous-leaved and pubescent- or scabrous-leaved forms; consequently leaf pubescence is of no diagnostic value, though some authors have used it as a key character. Paniculately or corymbosely branched plants of *L. ligulistylis*, *L. spherioidea*, and *L. squarrulosa* occur rather frequently, generally with normal spicate or racemose plants. In most cases these appear to be the result of insect injury. The transition in size from lower to upper leaves may be gradual or abrupt, some species showing distinct tendencies toward one or the other extreme, others displaying both extremes and all gradations between. Because of the amount of variation and overlap, it is not a reliable distinguishing feature, though it has been much used in characterising proposed new species and varieties. Even the number of florets per head, an extremely useful feature, cannot safely be used alone.

The necessity of considering characters in combination is the key to the whole complex. The break in a single character between two distinct species may be bridged by a third, obscuring the real value of that character. Thus *Liatris novae-angliae* with 30-80 florets per head is amply distinct from *L. squarrulosa* with 12-27, but *L. scariosa* with 21-40 fills in the gap. *Liatris scariosa* with 8-20 leaves is in turn amply distinct from *L. novae-angliae* with 25-60, but *L. ligulistylis* with 8-100 and *L. spherioidea* with 13-90 fill in the gap. This intrusion of foreign intermediates between distinct entities, and the occurrence of parallel variations, have between them given the *Liatris scariosa* complex the appearance of an inextricable jumble of forms, and led to the notorious difficulty in delineating genuine entities. Finally, a character of fundamental importance, the nature of the margins of the phyllaries (or involucral bracts), has apparently been overlooked or ignored by previous writers, with the exception of E. J. Alexander, in Small's *Manual of the Southeastern Flora*.

The present study has included an examination of specimens from the herbaria of the following institutions and individuals: the Deam Herbarium of Indiana University; O. A. Farwell, Lake Linden, Michigan; the Field Muse-

um of Natural History; the Gray Herbarium; Louisiana State University; the Milwaukee Public Museum; the University of Minnesota; the Missouri Botanical Garden; the New York Botanical Garden; the University of Pennsylvania; the Academy of Natural Sciences, Philadelphia; the Rocky Mountain Herbarium of the University of Wyoming; the University of West Virginia; and the University of Wisconsin. Grateful acknowledgment is made to the curators of these herbaria for their courtesies. In addition, helpful information and assistance in various ways have been received from Dr. J. F. Brenckle, Mellette, South Dakota; Dr. C. C. Deam, Bluffton, Indiana; Mr. Delzie Demaree, of Arkansas Agricultural and Mechanical College; Dr. N. C. Fassett, of the University of Wisconsin; Prof. W. P. Fraser, of the University of Saskatchewan; Dr. H. C. Greene, of the University of Wisconsin; Dr. Theodor K. Just, of the University of Notre Dame; Dr. G. F. Ledingham, Moose Jaw, Saskatchewan; Prof. E. H. Moss, of the University of Alberta; Mr. R. W. Pohl, of the University of Pennsylvania; and Mr. C. A. Weatherby, of the Gray Herbarium. Hall's Outline Map of North America (205 C), published by John Wiley and Sons, Inc., New York, was used in making the distribution maps. Completion of the paper has been made possible by financial aid from the Wisconsin Alumni Research Foundation.

Nearly two thousand specimens have been examined. Comparatively few of these were duplicates of widely distributed collections, and in a number of cases specimens bearing the same collection number were not identical. The customary citation of specimens has therefore been discarded in favor of a set of distribution maps, in the belief that no really useful purpose would be served by a cataloguing of specimens. Such a proceeding would scarcely justify taking the amount of space required.

The key is to species only. Three of the hybrids, \times *Liatris Gladewitzii*, \times *L. Weaveri*, and \times *L. fallacior*, differ from the proper members of the *L. scariosa* complex in having the pappus plumose instead of merely barbellate. The other two, \times *L. Deamii* and \times *L. Rosendahlia*, are mentioned at points where they might key out, but their identity can be satisfactorily determined only by comparison with specimens of the parent species, and consideration of the locality in which they were found.

KEY TO THE SPECIES

- Middle phyllaries coriaceous throughout, or with narrow scarious borders of uniform width; margins entire, or shallowly and evenly erose, ciliate or glabrous; phyllaries glabrous, hirsutulous, or cinereous on the back.
- Stems with 8-20 leaves or leafy bracts below the inflorescence; (heads usually 28-40-flowered; plants of the Appalachian Mountains and adjacent territory from southern Pennsylvania to Georgia).2. *L. scariosa*
- Stems with 20-85 leaves or leafy bracts below the inflorescence.
- Heads 30-80-flowered.
- Lower stem leaves mostly 0.5-2.5 cm. wide; plants of New England and New York.1. *L. novae-angliae*
- Lower stem leaves mostly 2.5-5.0 cm. wide; plants of the interior.1b. *L. novae-angliae* var. *Nieuwlandii*

Heads 12-29—flowered.

- Phyllaries glabrous or puberulent with loosely appressed hairs; achenes 3.5-5.0 mm. long. 3. *L. squarrulosa*
 Phyllaries densely cinereous with short, stiff, spreading hairs (rarely glabrous); achenes 5.0-6.0 mm. long. 4. *L. aspera*

Middle phyllaries with broad scarious borders of uneven width; margins irregularly lacerate, glabrous; phyllaries glabrous on the back (occasionally the outermost hirsutulous toward the base).

Heads 16-35—flowered, uniform in size; involucre 0.8-1.5 mm. high, the innermost phyllaries usually 8-13 mm. long; middle and outer phyllaries squarrose, the lowest commonly reflexed, all usually much crisped, the tips concave, with a semicircular crease or pucker, the scarious border sometimes completely folded under.

Heads horizontal or ascending, sessile or on straight peduncles; plants of general distribution in interior United States. 5. *L. spherioidea*

Heads nodding, on short curved peduncles; plants of eastern Texas and Louisiana. 5b. *L. spherioidea* var. *salutans*.

Heads 30-106—flowered, the terminal one distinctly larger than the rest; involucre 1.3-2.0 cm. high, the innermost phyllaries usually 12-18 mm. long; middle and outer phyllaries loose or appressed (only the outermost reflexed), flat or with spreading tips, occasionally slightly crisped (see also *×L. Deamii* and *×L. Rosendahlit*). 6. *L. ligulistylis*

1. *Liatris novae-angliae* (Lunell) stat. nov.

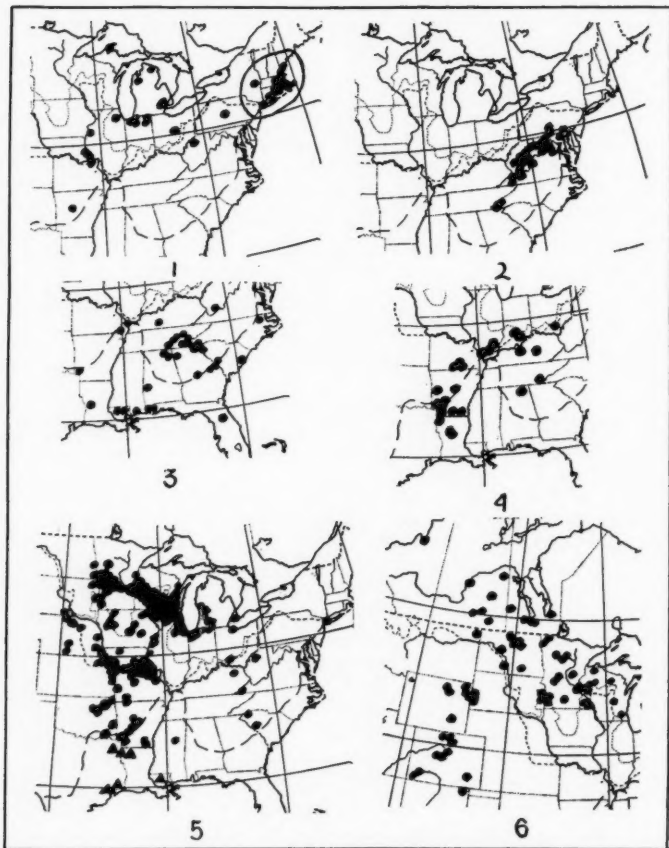
Lacinaria scariosa var. *novae-angliae* Lunell, Amer. Midl. Nat. 2:172 and 177, 1912. *Liatris scariosa* and *Lacinaria scariosa* of authors, in part; not *Serratula scariosa* L.

White-flowered form: *Liatris novae-angliae* f. *albiflora*, f. nov. Corollis albis. TYPE: Boxford, Massachusetts, A. L. Page, Sept. 10, 1909 (in Gray Herbarium).

Stem 35-100 cm. tall (usually above 50 cm.), striate, glabrous below, pubescent above with loose or appressed, whitish, straight or crisped hairs; with 25-60 leaves or leafy bracts below the inflorescence. Leaves usually glabrous, sometimes scabrous or pubescent; generally firm and somewhat succulent; the lowest with petioles 2-7 cm. long, and linear to lanceolate blades 0.5-2.5 cm. wide by 7-12 cm. long. Middle and upper leaves gradually reduced to linear or narrowly lanceolate sessile leafy bracts, those just below the inflorescence 1-4 mm. wide by 5-30 mm. long. Heads 6-30 (-60) per plant, with 30-80 florets per head; on rather closely ascending, straight or slightly flexuose peduncles (4-) 7-50 mm. long. Involucre hemispherical, 12-17 mm. high. Phyllaries glabrous or hirsutulous on the back, glabrous or more commonly ciliate on the entire or shallowly and evenly erose margins; green to dark red. Outer phyllaries lanceolate or ovate-lanceolate, appressed to squarrose, 1-4 mm. wide by 4-8 mm. long. Middle phyllaries lanceolate or ovate-lanceolate, flat, appressed or closely ascending, 3.5-6.0 mm. wide by 8-12 mm. long. Inner phyllaries oblong or linear-oblong, flat, erect, 1.25-3.50 mm. wide by 11-17 mm. long. Corollas 7-10 mm. long, the lobes 2-3 mm. long, lanceolate or deltoid-lanceolate, glabrous, often resin-dotted. Achenes black-brown at maturity, 5.5-8.0 mm. long, 1.0-1.5 mm. wide at the summit, tapered to the base,

8-10 ribbed, pilose with spreading hairs 0.1-0.2 mm. long. Pappus hairs about 25-35, 7-9 mm. long, barbellate; whitish, tawny, or dull purplish.

Dry or sandy soil, especially near the coast, southern Maine to coastal New York and Long Island, extending inland in the Connecticut Valley; found also near Albany, New York (map 1).



Map 1. Distribution of *Liatris novae-angliae* (inside circle) and var. *Nieuwlandii* (outside circle). Map 2. Distribution of *Liatris scariosa*. Map 3. Distribution of *Liatris squarulosa*. Map 4. Distribution of *Liatris aspera*. Map 5. Distribution of *Liatris spherioidea* (dots) and var. *salutans* (triangles). Map 6. Distribution of *Liatris ligulistylis*.

Authors have uniformly assumed that this plant was the true *Liatris scariosa*, in spite of the fact that the name *scariosa* is quite inappropriate for it, and the Linnaean type locality was Virginia, where this species does not occur. As a result, it enjoys the distinction, unique in this complex, of having had only one name applied to it, and of never having had a specific name of its own. It is a very common plant in southeastern New England, especially on and near Cape Cod, where it runs to forms with very narrow, crowded leaves. Inland it is somewhat local, and tends to have larger and fewer leaves. The white-flowered form is apparently rare, only three collections having been seen: one from New York and two from Massachusetts.

1b. *Liatris novae-angliae* var. *Nieuwlandii* (Lunell) comb. nov.

Lacinaria scariosa var. *Nieuwlandii* Lunell, Amer. Midl. Nat. 2: 171 and 176, 1912. *L. scariosa* var. *Nieuwlandii* f. *borealis*, f. *gracillima*, and f. *versicolor* Lunell, l. c. *L. scariosa*, *Nieuwlandii septentrionalis* Lunell, l. c. 264.

White-flowered form: *Liatris novae-angliae* var. *Nieuwlandii* f. *alba*, f. nov. Corollis albis. TYPE: Nickle Plate Railway 2½ miles north of Rochester, Fulton Co., Indiana, Deam 43670, Sept. 17, 1926 (in Deam Herbarium, Indiana University).

Sweet-scented form: *Liatris novae-angliae* var. *Nieuwlandii* f. *trilisioides* (Farwell) stat. nov. *Lacinaria scariosa* var. *trilisioides* Farwell, Rep. Mich. Acad. Sci. 17:170-171, 1916.

Similar to the species, but the leaves averaging fewer (20-50), larger (lower blades up to 5 cm. wide), and less reduced above; outer phyllaries often enlarged and foliaceous; and stems frequently densely pubescent to the base. In dry rocky or sandy soil, central Pennsylvania, West Virginia, Ohio, Michigan, Indiana, Illinois, Missouri, and Arkansas (map 1). Lack of data on most herbarium specimens makes it impossible to tell the distribution or frequency of the sweet-scented form; it is definitely known only from southeastern Michigan and central Pennsylvania. The white-flowered form is known only from northern Indiana.

×*Liatris Deamii* (Lunell) comb. nov.; stat. emend.

Lacinaria Deamii Lunell, Amer. Midl. Nat. 2: 169, 1912. *L. scariosa* var. *intermedia* Lunell, l. c. 173 and 177. *Lacinaria scariosa media* Lunell, l. c. 264. *Liatris scariosa* var. *Deamii* Peattie, Amer. Midl. Nat. 10: 132, 1926. (*Liatris novae-angliae* var. *Nieuwlandii* × *L. spherioidea*.)

White-flowered form: *Liatris Deamii* f. *albina*, f. nov. Corollis albis. TYPE: Bear Lake, Wolf Lake, Noble Co., Indiana, N. C. Fassett 21207, Sept. 11, 1941 (in Herb. University of Wisconsin). Growing with the ordinary form.

Showing various combinations of parental characters; the majority of specimens with the relatively few ample leaves and few large peduncled heads of *L. novae-angliae* var. *Nieuwlandii*, and the crisped phyllaries with lacerate

scarious margins of *L. spherioidea*. Apparently not rare in northern Indiana and southern Michigan; also found in West Virginia, Missouri, and Arkansas.

2. *LIATRIS SCARIOSA* (L.) Willd., Sp. Pl. 3:1634, 1804.

Serratula scariosa L., Sp. Pl. 2: 818, 1753. *Lacinaria scariosa* Hill, Hort. Kew. 70, 1769 (nomen genericum rejiciendum). *Liatris borealis* Nutt. ex Macnab, Edinburgh New Philos. Jour. 19: 60, 1835. *Lacinaria scariosa* var. *virginiana* Lunell, Amer. Midl. Nat. 2: 172 and 177, 1912. *L. scariosa borealis* Lunell, l. c. 264.

Stem 30-80 cm. tall (usually below 60 cm.), striate, glabrous or pubescent with crisped hairs; with 8-20 leaves or leafy bracts below the inflorescence. Leaves glabrous or pubescent, the lower with petioles 2-10 cm. long, and broadly lanceolate or rhombic- or ovate-lanceolate blades 2.5 cm. wide by 6.0-12.5 cm. long. Middle and upper leaves rather abruptly reduced to oblong-lanceolate or lanceolate sessile leafy bracts, those just below the inflorescence 3-15 mm. wide by 10-40 mm. long. Heads 4-25 (-30) per plant, with (21-) 28-40 florets per head; on straight or arcuate, stiffly divergent, ascending to horizontal or recurved peduncles 8-50 mm. long. Involucres roughly hemispherical, broadly rounded at base, 9-12 mm. high. Phyllaries glabrous or puberulent on the back, with distinct though often very narrow scarious borders, the margins entire and glabrous or ciliate; dark green, rose red, or purple; loose and more or less crisped, the outer reflexed. Outer phyllaries broadly deltoid to oblong-lanceolate, 2.0-3.5 mm. wide by 3.5-6.0 mm. long. Middle phyllaries oblong, oblong-obovate, or spatulate, 1.5-4.0 mm. wide by 6-11 mm. long. Inner phyllaries narrowly oblong or linear, 1.0-2.5 mm. wide by 9-12 mm. long. Corollas 7-9 mm. long, the lobes 2-3 mm. long, deltoid-lanceolate, glabrous, often resin-dotted. Achenes blackish brown at maturity, 5-6 mm. long, 1.0-1.7 mm. wide at the summit, tapered to the base, 8-10-ribbed, pilose with spreading or ascending-spreading white hairs 0.1-0.2 mm. long. Pappus hairs about 20-25, 6-8 mm. long, barbellate, yellowish to dull purple.

Dry rocky slopes, especially shale barrens, Appalachian Mountains (including the Blue Ridge) from southern Pennsylvania through Maryland, West Virginia, Virginia, and North Carolina, to the Georgia boundary; extending onto the inner Coastal Plain in Virginia (map 2).

It is possible that the name *Liatris scariosa* is not properly applied to this plant. The type locality given by Linnaeus was simply "Virginia," and synonyms are cited from Banister, Gronovius, and Plukenet. Three species occur in the region of the type locality: the present one, *L. spherioidea*, and *L. squarrulosa*. Of these, *L. squarrulosa* lacks the scarious margins of the phyllaries, and so would hardly qualify as the type of the specific name *scariosa*, taken by Linnaeus from the description by Plukenet ("floribus scariosis"). *Liatris spherioidea* is less easily disposed of. Since it is found only in the western Appalachians in the latitude of Virginia, however, and is rare there, while the species here called *Liatris scariosa* is the most common and widespread one in the region, it is rather unlikely that *L. spherioidea* could have been the plant described by Linnaeus. Furthermore the phrase "pedunculis

lateralibus, elongatis" would not apply to most specimens of *L. spherioidea*, which typically has sessile or short-peduncled heads; but would aptly describe a typical specimen of the *L. scariosa* of this treatment. A final decision on the question must await an examination of the specimen on which Linnaeus based the remarks of his own, appended to the list of references cited by him. These references (including the Plukenet figure) and Linnaeus's own comments are insufficient basis for any positive conclusions. It is entirely possible that the various authors were not all describing the same plant.

3. LIATRIS SQUARRULOSA Michx., Fl. Bor.-Am. 2:91, 1803.

Liatris heterophylla R. Br. apud Ait., Hort. Kew. 2nd ed. 4:503, 1812. *Liatris scariosa* of Elliott, Sk. 2: 280, 1824; not *Serratula scariosa* L. *Liatris scariosa* var. *confertiflora*, var. *diversifolia*, var. *foliosa*, and var. *lanceolata* Ell., l. c. 281. *Liatris scariosa* var. *squarrulosa* A. Gray, Syn. Fl. 1 pt. 2: 110, 1884. *Laciniaria scariosa* var. *squarrulosa* Small, Mem. Torr. Bot. Club 4: 128, 1894. *Laciniaria Ruthii* Alexander apud Small, Man. S. E. Fl. 1335 and 1508, 1933 (not *L. Ruthii* Bush, Amer. Midl. Nat. 12:316-317, 1931). *Laciniaria Tracyi* Alexander apud Small, l.c. 1335 and 1508.

Stem 30-105 cm. tall, striate, glabrous or pubescent with straight and appressed or crisped hairs; with 20-85 leaves or leafy bracts below the inflorescence. Leaves glabrous or pubescent, the lower with petioles 2.5-12.0 cm. long, and linear-lanceolate to broadly lanceolate blades 0.2-5.0 cm. wide by 8-22 cm. long. Middle and upper leaves gradually or rather abruptly reduced to linear-lanceolate sessile leafy bracts, those just below the inflorescence 1-6 mm. wide by 7-60 mm. long. Heads 3-20 per plant, with 12-27 florets per head; sessile or on ascending or spreading straight peduncles 1-12 mm. long (or much longer in abnormal paniculately branched individuals). Involucres turbinate, rounded or somewhat pointed at base, 8-14 mm. high. Phyllaries coriaceous throughout, glabrous or hirsutulous on the back, glabrous or ciliate on the entire margins, yellow green to dark olive green with rose-red to dark purple-red tips and edges, all but the outermost usually erect or appressed. Outer phyllaries deltoid-lanceolate, 1.0-3.5 mm. wide by 2.5-6.0 mm. long. Middle phyllaries oblong-lanceolate, oblanceolate, or oblong-spatulate, 1.5-4.0 mm. wide by 4-11 mm. long. Inner phyllaries narrowly oblong to linear-spatulate, 1-2 mm. wide by 7-13 mm. long. Corollas 7.5-11.0 mm. long, the lobes 2.0-3.5 mm. long, deltoid-lanceolate or lanceolate, glabrous, often resin-dotted. Achenes black-brown or black at maturity, 3.5-5.0 mm. long, 0.8-1.2 mm. thick at the summit, tapered to the base, 8-10—ribbed, pilose with ascending or spreading hairs 0.1-0.2 mm. long. Pappus hairs about 30-40, 6-9 mm. long, barbellate; white, creamy, or gray, sometimes purple-tipped.

Thickets or open ground, in dry usually sandy or rocky soil, Florida to Louisiana, southeastern Missouri, Kentucky, southern West Virginia, and North Carolina (map 3).

Two tendencies are exhibited by the rather scanty available collections of this species, and on further investigation it may prove desirable to accord them recognition as varieties. Plants from the outer Coastal Plain, particularly

those from the Gulf Coast, are mostly very narrow-leaved, with blades 0.2-1.8 cm. wide. The type specimen for *Lacinaria Tracyi* Alexander represents this narrow-leaved form. Plants from the interior are mostly broad-leaved, the blades of the lower leaves (0.6-)1.5-5.0 cm. wide. The types of *Liatris squarrosa* (from "Basse Caroline," photo in Gray Herb.) and *Lacinaria Ruthii* Alexander (from eastern Tennessee) represent the broad-leaved form. There is so much variation and such considerable overlap in the measurements that I am unwilling to give the two forms nomenclatorial recognition without additional collections and field investigation. It is possible that hybridization with Coastal Plain species of the *Liatris graminifolia* and related groups has contributed to the prevalence of narrow-leaved plants in outer Coastal Plain collections.

A collection made on chalk prairie in Greene Co., Alabama, by R. M. Harper (no. 3137, in Gray Herb. and Herb. N. Y. Bot. Gard.) requires special mention. It has the small heads and narrow leaves characteristic of outer Coastal Plain *L. squarrosa*, but is densely cinereous throughout, as is characteristic of *L. aspera*. One or two Louisiana specimens show similar combinations of characters. Again, no satisfactory disposition of these plants can be made without more extensive collecting and field investigation. They are included with *L. squarrosa* in map 3.

4. *LIATRIS ASPERA* Michx. Fl. Bor.-Am. 2:91, 1803.

Lacinaria scabra Greene, Pittonia 4: 317-318, 1901. *Liatris scabra* K. Schum., Justs Bot. Jahresb. 29 pt. 1: 569, 1903. *Lacinaria Shortii* Alexander apud Small, Man. S. E. Fl. 1335 and 1508, 1933.

Stem 60-150 cm. tall, striate, densely cinereous with short, stiff, widely spreading hairs (occasionally with subappressed hairs, or rarely glabrous); with 20-70 leaves or leafy bracts below the inflorescence. Leaves densely cinereous on both surfaces, rarely glabrous; the lower with petioles 2-11 cm. long and lanceolate to ovate blades 1.7-3.5 cm. wide by 10-18 cm. long. Middle and upper leaves gradually reduced to lanceolate or oblong-lanceolate sessile leafy bracts, those just below the inflorescence 3-8 mm. wide by 20-40 mm. long. Heads 15-40(-55) per plant, with 18-29 florets per head; sessile or on short spreading-ascending or arcuate and slightly recurved peduncles 1-12 mm. long. Involucres oblong or oblong-campanulate, 10-14 mm. high. Phyllaries coriaceous throughout, densely cinereous (rarely glabrous), copiously resin-dotted, with entire ciliate margins, gray green with vinous purple tips, the outer reflexed, the middle erect with abruptly squarrose tips. Outer phyllaries deltoid-lanceolate, 2.0-3.5 mm. wide by 4-6 mm. long. Middle phyllaries oblong, oblong-obovate, or spatulate with nearly orbicular tips and a claw-like base, 3-4 mm. wide by 8-11 mm. long. Inner phyllaries narrowly oblong, 1.5-3.0 mm. wide by 9-12 mm. long. Corollas 6.5-9.5 mm. long, the lobes 2.0-2.5 mm. long, lanceolate or deltoid-lanceolate, glabrous, often resin-dotted. Achenes black-brown at maturity, pilose with white ascending hairs, 0.2-0.3 mm. long. Pappus hairs about 30-40, 7.0-8.5 mm. long, barbellate, light or dark purplish (sometimes tawny below the tips).

Open oak woods (especially with *Quercus Prinus*), often in clay soil; south of the limits of glaciation and north of the Coastal Plain (except in Louisiana), Ohio and southern Missouri to northern Alabama and Louisiana (map 4).

As with *Liatris scariosa*, the identity of this species and the next have been determined provisionally by a combination of deduction and conjecture. The type locality for *L. aspera* was "in regione Illinoensi." Again there are three species which occur in the region of the type locality: the present one, *L. spherioidea*, and *L. novae-angliae* var. *Nieuwlandii*. The last can be eliminated because of its peduncled heads; Michaux' description calls for a spike with "floribus . . . sessilibus." The type locality for *L. spherioidea* is given as "in pratis Illinoensibus et in excelsis montibus Carolinae." The only species having such a range is *L. spherioidea* as treated here. One more possibility remains: that *L. aspera* was merely a rough-leaved form of *L. spherioidea* (*L. spherioidea* f. *asperifolia* of this treatment). There is no definite evidence either for or against this interpretation, other than the assumption that Michaux would not be likely to describe two forms as two species together, giving entirely different wordings to the descriptions for each. The selection of the name *scabra* for this species by Greene is suggestive, as is the use of the name *spherioidea* for the other by Michaux, and his omission of the habitat "pratis" for *L. aspera*. Final decision of course must await an examination of the types. If *L. aspera* should prove to be the rough-leaved form of *L. spherioidea*, the former name must be adopted. According to the International Rules, the first author to unite two entities of coordinate rank, simultaneously published, must be followed. Consequently although Alexander's name *Laciniaria aspera* var. *spherioidea* is invalid on three separate counts (no basynym or reference was given, there were numerous other earlier names for the same plant in the varietal category, and *Laciniaria* is a *nomen rejiciendum*), his subordination of *L. spherioidea* is binding.

A collection from Warren Co., Indiana, Deam 9986 (co-type of *Laciniaria scariosa* var. *praesignis* Lunell, in Herb. University of Minnesota), is possibly an aberrant individual of this species. The involucre has the characteristic dense cinereous pubescence, but the stem pubescence is appressed and the heads oblong, suggesting hybridization with *L. spherioidea* or possibly *L. novae-angliae* var. *Nieuwlandii*.

5. LIATRIS SPHERIOIDEA Michx., Fl. Bor.-Am. 2:91, 1803.

Liatris scariosa and *Laciniaria scariosa* of authors, in large part; not *Serratula scariosa* L. *Liatris scariosa* var. *intermedia* Ell., Sk. 2: 281, 1824. *Laciniaria aspera* of Greene, Pittonia 4: 318, 1901; not *Liatris aspera* Michx. *Laciniaria alata* A. Nels., Bot. Gaz. 31: 405, 1901. *Liatris alata* K. Schum., Justs Bot. Jahresb. 29 pt. 1: 569, 1903. *Laciniaria scariosa* var. *aspera* and var. *spherioidea* Farwell, Rep. Mich. Acad. Sci. 15: 188, 1913. *Liatris aspera* of Rydb., Fl. Prairies & Plains, in part; not *L. aspera* Michx. *Laciniaria aspera* var. *spherioidea* Alexander apud Small, Man. S. E. Fl. 1334, 1933. Also 14 varieties described by Lunell (see appendix).

White-flowered form: *Liatris spherioidea* f. *Benkei* (Macbride) comb.

nov. *Liatris scariosa* f. *Benkei* Macbride, Field Museum Publ. Bot. Ser. 4:124, 1927.

Rough-leaved form: *Liatris spherioidea* f. *asperifolia*, f. nov. Foliis scabris. TYPE: Roadside, Liberty Ridge, Lancaster, Grant Co., Wisconsin, N. C. Fassett 13469, Sept. 3, 1930 (in Herb. University of Wisconsin).

Stem 40-120 cm. tall, striate, glabrous throughout or pubescent above; with 13-90 leaves or leafy bracts below the inflorescence. Leaves glabrous or scabrous-pubescent (f. *asperifolia*), usually strongly punctate; the lower with petioles 1-16 cm. long, and lanceolate, oblanceolate, or rhombic-lanceolate blades 0.7-4.5 cm. wide by 6-22 cm. long. Middle and upper leaves gradually reduced to oblong, oblong-lanceolate, or linear sessile leafy bracts, those just below the inflorescence 0.8-7.0 mm. wide by 8-70 mm. long. Heads 6-80 (most commonly 7-40) per plant, with 16-35 (in one specimen -45) florets per head; sessile or on short spreading or ascending peduncles 1-20 (-50) mm. long (or longer in occasional paniculately branched individuals). Involucres ovoid ("spheroidal") or oblong-campanulate, 8-15 mm. high. Phyllaries glabrous, often resin-dotted, loosely spreading to squarrose, all cupped or crispate, with a semicircular pucker or crease near the top, with conspicuous irregularly lacerate scarious borders (the scarious borders sometimes completely folded under, so that the phyllary apparently has a smooth firm edge); body of the phyllaries bright green or yellow green, the borders white, pink, rose-red, or sometimes dark purple-red. Outer phyllaries deltoid-lanceolate, ovate, or oblong, 1.5-3.5 mm. wide by 2-5 mm. long. Middle phyllaries oblong, obovate, or spatulate, 3.0-6.5 mm. wide by 6-12 mm. long. Inner phyllaries narrowly oblong- or linear-spatulate, 1.0-2.5 mm. wide by 8.2-13.0 (in one specimen -14.0) mm. long. Corollas 7.0-9.5 mm. long, the lobes 2.5-3.0 mm. long, lanceolate, glabrous, often resin-dotted. Achenes tawny-brown to black-brown at maturity, 5-6 mm. long, 0.5-0.8 mm. wide at the summit, tapered to the base, 8-10-ribbed, pilose with spreading-ascending white hairs 0.2-0.3 mm. long. Pappus hairs about 30-40, 6.0-7.5 mm. long, barbellate; white, gray, yellowish, or purplish.

Prairies and dry open ground, or in open jack pine or oak woods, in sandy soil, rarely in silt or clay loam; very common in the Middle West from southern Ontario and northern Ohio to southeastern South Dakota, south to central Oklahoma, southern Arkansas, and northern Mississippi; locally in southern Ohio, eastern Kentucky, western West Virginia and Virginia, and western South Carolina; and a single early collection from Long Island, New York (map 5).

Judging from the number of herbarium specimens, this is the most abundant species of the complex. It is a variable one, and some of the forms deserve special mention. Smooth- and rough-leaved forms occur throughout the range of the species, but there is a tendency for the former to predominate in the Appalachian region, while f. *asperifolia* is the common form in the Middle West. The number of leaves varies greatly; a noteworthy extreme is a collec-

tion from Greenville Co., South Carolina (Wherry & Pennell 14236, in Herb. Phila. Acad.), which has 13 leaves below the inflorescence, with broad blades, and heads on short rigid horizontal peduncles, all characteristics of the Appalachian *L. scariosa*. Some Oklahoma collections have heads larger than average, with long, oblong phyllaries. The type of *Lacinaria alata* A. Nels. represents the extreme of this form, with 45 florets in one head, and inner phyllaries up to 14 mm. long. In addition to these local variants, there are a few others found in all parts of the range: paniculately branched plants (usually the result of insect injury), and plants with very dark purple-red involucre. The albino, f. *Benkei*, is not rare in the upper Mississippi Valley states.

There is an early collection in the Torrey Herbarium (in Herb. N. Y. Bot. Gard.) from Long Island, New York; a duplicate of this was doubtless the type of *Liatris scariosa* var. *intermedia* Ell. (Sk. 2:281, 1824). If the plant was actually native there, this represents a peculiarly isolated station for it. It is not impossible that it was a casual introduction, though the early date makes this seem unlikely. It has not been collected there since, and the nearest stations known for it now are in Ohio and West Virginia.

5b. *Liatris spherioidea* var. *salutans* (Lunell) comb. nov.

Lacinaria scariosa var. *salutans* Lunell, Amer. Midl. Nat. 2: 171 and 176, 1912.

Heads nodding, on sandy curved peduncles; otherwise like the species. Prairies or sandy soil, eastern Texas and Louisiana (map 5); apparently the only form of the species in these states. One or two specimens do not show distinctly nodding heads, but since this character may be affected by pressing and by the age of the plant, they have been ignored in compiling the map.

×*Liatris Gladewitzii* (Farwell) Farwell, comb. nov.

Lacinaria Gladewitzii Farwell, Amer. Midl. Nat. 10: 43, 1926. (*Liatris cylindracea* × *L. spherioidea*).

Sandy soil and prairie bluffs; Wisconsin, Michigan, and southern Ontario. Showing various combinations of parental characters; the following description is based on the type (from Rochester, Oakland Co., Michigan; in herb. O. A. Farwell).

Stem glabrous, striate, up to 93 cm. tall. Leaves glabrous, the lower narrowed to petiole-like bases, with 3-nerved, narrowly oblong or oblong-lanceolate blades up to 1.4 cm. wide by 22 cm. long. Middle and upper leaves gradually reduced to leafy bracts, those just below the inflorescence 2 mm. wide by 35 mm. long. Inflorescence a spicate raceme 15-30 cm. long, the rachis and peduncles pubescent; heads 9-23 per spike, borne in the axils of short leafy bracts or of the upper leaves, closely ascending. Involucre oblong- or cylindrical-campanulate, 16-17 mm. high, with 20 florets in one head. Phyllaries glabrous on the back, ciliate on the margins, the middle and inner erose at the tip; imbricated in 6-7 rows. Outer phyllaries oblong or oblong-ovoid, apiculate, 2.5-3.0 mm. wide by 4 mm. long, with narrow scarious margins

around the tips. Middle phyllaries oblanceolate or narrowly spatulate, 4-5 mm. wide by 10-12 mm. long, emarginate, with broader pink or rosy scarious borders. Inner phyllaries narrowly oblong, 1.5-3.5 mm. wide by 14-16 mm. long, with rounded scarious tips. Corollas hispid-pubescent within, deeply lobed; styles conspicuously exserted. Achenes (immature) blackish brown, 6.5 mm. long, 1.5 mm. wide at the summit, tapered to the base, striate or ribbed, pilose with ascending hairs. Pappus hairs 10 mm. long, plumose, silvery gray with a purple tinge.

Two other collections have been seen, both in the Herbarium of the University of Wisconsin: Sandy ground, Rondeau Provincial Park, Kent Co., Ontario, *N. C. Fassett 15026*, Sept. 5, 1931 (growing with *L. spherioidea*). Dry summit of limestone bluff, Prairie du Chien, Crawford Co., Wisconsin, *Fassett 4478*, Aug. 20, 1927. Both have stems pubescent except near the base, less than half as tall as the type (30-40 cm. high), with proportionately smaller leaves; heads 13-15 mm. high, with 29 and 31 florets; those of the Wisconsin specimen broader than in the others, almost hemispherical, and with more pronounced scarious margins on the phyllaries.

×*Liatris Weaveri*, sp. nov.

(*Liatris punctata* × *L. spherioidea*).

TYPE: "From seeds sent by Dr. Weaver to Dr. Gaiser, no. 16," Locarina, Nebraska, Sept. 15, 1933 (in Herb. Missouri Bot. Gard., Cat. no. 1063654). Known only from the type specimen and two duplicates (numbered 4 and 17, also in Herb. Mo. Bot. Gard.).

Caulis 45-50 cm. altus, infra glaber, supra pubescens. Folia glabra, utrinque punctata, inferiora subpetiolata, lineari-lanceolata. Inflorescentia spicata, infra foliosa, media bracteata. Involucri anguste oblongo-campanulata, 13 mm. alta, sessilia; flores 9-15. Phyllares imbricati, interiores margine scariosi. Pappus plumosus.

Stem 45-50 cm. high, sulcate-striate, glabrous below, pubescent with loose crisped hairs toward the inflorescence. Leaves glabrous, punctate on both surfaces, the lower tapered to a short petiole-like base, with linear-lanceolate blades; the middle and upper gradually reduced to leafy bracts, extending well into the inflorescence, exceeding or equalling the involucri except in the terminal $\frac{1}{4}$ of the spike, those at the base of the inflorescence 2 mm. wide by 35 mm. long. Involucri narrowly oblong-campanulate, 13 mm. high, sessile, ascending, with 9-15 florets. Phyllaries imbricate in 4-6 rows, the middle and inner oblong or oblong-lanceolate, rounded at the tip, with prominent scarious white or rosy borders; the outer wholly green, deltoid or deltoid-lanceolate. Corollas 9.0-11.5 mm. long, the lobes 3.0-3.5 mm. long, glabrous, resin-dotted. Achenes (immature) 5.5-6.0 mm. long, 1 mm. wide at the summit, tapered to the base, 10-ribbed, pilose with ascending hairs 0.2-0.3 mm. long. Pappus hairs about 30-35, 7.5-9.0 mm. long, tawny or yellowish, plumose, the branch hairs about 0.5 mm. long.

6. *LIATRIS LIGULISTYLIS* (A. Nels.) K. Schum., Justs Bot. Jahresb. 29 pt. 1: 569, 1903.

(This combination also later published as new by A. Nels. in Coult. & Nels., New Man. Rocky Mt. Botany 488, 1909; and Rydb., Brittonia 1:100, 1931.)

Lacinaria ligulistylis A. Nels., Bot. Gaz. 31: 405, 1901. *Liatris borealis* Paxton's Mag. v. t. 27, 1836; not *L. borealis* Nutt. ex Macnab, 1835 (which is *L. scariosa*). *Lacinaria scariosa* f. *globosa* and f. *uniflora* Sheldon, Quart. Bull. Univ. Minn. 1: 27, 1892. *Lacinaria scariosa* var. *corymbulosa* Sheldon, Minn. Bot. Studies 1 (Bull. Minn. Geol. Surv. 9, Bot. Ser. II): 77-78, 1894. *Lacinaria formosa* Greene, Leaf. 1: 149, 1905. *Liatris Haywardii* and *L. Herrickii* Rydb., Brittonia 1:99-100, 1931. *Lacinaria aspera* of Rydb., Fl. Rocky Mts., and *Liatris aspera* of Rydb., Fl. Prairies and Plains, in part; not *Liatris aspera* Michx. *Liatris scariosa* of authors, in part; not *Serratula scariosa* L. Also 19 varieties described by Lunell (see appendix).

White-flowered form: *Liatris ligulistylis* f. *leucantha*, f. nov. Corollis albis. TYPE: On prairies, Leeds, North Dakota, J. Lunell, Sept. 9, 1908 (in Herb. University of Minnesota; specimen marked *b* on sheet).

Stem 18-110 cm. tall, striate, glabrous below, appressed pubescent above; with 8-100 leaves or leafy bracts below the inflorescence. Leaves glabrous, scabrous, or pubescent; the lower with petioles 3-6 cm. long, and linear-lanceolate, lanceolate, or rhombic-lanceolate blades 0.5-4.0 cm. wide by 5-21 cm. long. Middle and upper leaves rather abruptly reduced to linear- or oblong-lanceolate sessile leafy bracts, those just below the inflorescence 1-3 mm. wide by 8-30 mm. long. Heads 1-35 (most commonly 3-10) per plant, with 30-106 florets per head; on peduncles 0.2-2.5 (-5.0) cm. long. Involucre broadly campanulate or hemispherical, 13-20 mm. high. Phyllaries glabrous, plane or with spreading tips, rarely slightly crispate, with prominent lacerate scarious borders; body of the phyllary bright green, olive, or brown, the border rose-red or rose-purple, occasionally white, pink, or brown. Outer phyllaries deltoid-lanceolate, oblong-lanceolate, or oval, 2-5 mm. wide by 4-7 mm. long. Middle phyllaries oblong, oblanceolate, or obovate, 3-5 mm. wide by 7-12 mm. long. Inner phyllaries linear, linear-spatulate, or oblong, 1.5-3.0 mm. wide by 11.8-18.5 mm. long. Corollas 7.5-10.5 mm. long, the lobes 2.0-2.5 mm. long, deltoid-lanceolate, glabrous, frequently resin-dotted. Achenes at maturity black-brown, 5.0-7.5 mm. long, 1.0-1.6 mm. wide at the summit, tapered to the base, 8-10-ribbed, hirsute with spreading-ascending white hairs 0.1-0.2 mm. long. Pappus hairs about 20-30, 6-11 mm. long, barbellate, pale or rusty purple, sometimes tawny below the tip.

In the Rocky Mountains from northern New Mexico through Colorado and Wyoming; in the Black Hills of South Dakota and in adjacent Wyoming; and across the northern prairies and plains from central Alberta and north-eastern Montana through Saskatchewan, Manitoba, North Dakota, and Minnesota to northwestern Wisconsin, with an outlying station in southeastern Wisconsin; also adventive along roadsides and railroads in various parts of Wisconsin (map 6).

In New Mexico and Colorado this plant is found in mountain meadows, preferring moist soil, and reaches an altitude of 8000 ft. (2500 m.). In north-eastern Wyoming and the Black Hills it grows in open dry pine woods. In central Alberta and central Minnesota it is found in sand, in open jack pine woods. In Wisconsin (where native), most of Minnesota, extreme eastern South Dakota, North Dakota, and the Prairie Provinces of Canada, it prefers damp soil, either sand or clay, growing in low prairies and around the borders of sloughs and lakes; less often it is found in dry prairies, and then usually in heavy soil. In Wisconsin, particularly in the northern part of the state, it is adventive in dry usually sandy soil, along railroads and roadsides.

The geographic range of the species follows a pattern characteristic of a number of Rocky Mountain plants: e.g., *Aster coerulescens* and *Erigeron glabellus*. Some others have generally similar ranges but with lesser or greater extensions eastward: *Erigeron pumilus* occurs as far as Manitoba; *Poa interior* all the way to Quebec. All are plants of the northern, glaciated part of the prairies and plains, suggesting that this region has served as an avenue for eastward migration. It is interesting to note that the greater part of the range of *Liatris ligulistylis* lies in glaciated territory, and that it is now actively extending its range eastward.

×*Liatris Rosendahlia* Rydb., Brittonia 1:100, 1931; stat. emend.

(*Liatris ligulistylis* × *L. spherioidea*).

Showing various combinations of parental characters; often difficult to distinguish from one or the other parent. Rather frequent in parts of Minnesota and Wisconsin where the parent species are found in close proximity.

In southeastern Wisconsin, *Liatris ligulistylis* comes into flower ten to twenty days ahead of *L. spherioidea* (end of July or beginning of August), but there is an overlap in blooming which may last several weeks. It grows in low prairie meadows, while the latter prefers dry prairie, in sandy soil or on rocky hillsides. In the field the two are quite distinct; the rather few-headed racemose inflorescence, large terminal head, darkly colored involucre, and earlier flowering of *L. ligulistylis* contrasting with the densely spicate inflorescence, uniform heads, light colored involucre with crisped phyllaries, and later flowering of *L. spherioidea*. In the herbarium, where the general facies is lost, and there may be an overlap in almost every specific character, the distinctness is not always so obvious. *L. ligulistylis* usually responds somewhat differently to insect injury than does *L. spherioidea*. The inflorescence may become congested and club-shaped, or it may become corymbose through the elongation of the lower peduncles. Such plants form the basis of several of Lunell's varieties.

×*Liatris fallacior* (Lunell) Rydb., Fl. Prairies and Plains 780, 1932; stat. emend.

Laciniaria fallacior Lunell, Amer. Midl. Nat. 5: 38, 1917. *L. fallacior* var. *celosoides* Lunell, l. c. (*Liatris ligulistylis* × *L. punctata*).

Combining the enlarged terminal head and broad, scarious-margined phyllaries of *L. ligulistylis* with the spicate inflorescence, few-flowered heads, plumose pappus, and punctate and ciliate phyllaries of *L. punctata*. For further description, see the references cited.

APPENDIX: INDEX OF LUNELL'S VARIETIES

The following names were published as varieties of *Lacinaria scariosa* by Lunell in a series of papers in the *American Midland Naturalist* from 1911 to 1919. Most of the types (the majority now in the Herbarium of the University of Minnesota, with some in the Deam Herbarium of the University of Indiana) have been examined; the identity of a few has been deduced from the published description and type locality. For convenience they are listed together here in alphabetical order, with the volume and page in the *American Midland Naturalist* where described, and their proper identity according to the present treatment.

angustata (2: 92, 93)—*ligulistylis*.
 annuens (5: 40)—*ligulistylis*.
 basilaris (2: 92, 93)—*ligulistylis*.
 borealis (2: 160, 162)—*scariosa*.
 brachiata (2: 264, 162)—*spherioidea*.
 Chandonnetii (2: 160, 162)—*spherioidea*
 or *×Rosendahlia*.
 composita (5: 40)—*ligulistylis*.
 crista-galli (5: 40)—*ligulistylis*.
 exuberans (5: 39)—*ligulistylis*.
 immanis (5: 40)—*ligulistylis*.
 inconcinna (5: 241)—*ligulistylis*.
 insolens (5: 40)—*ligulistylis*.
 intermedia (2: 173, 177)—*×Deamii*.
 media (2: 264)—*×Deamii*.
 multiplex (2: 92, 93)—*ligulistylis*.
 nictitans (2: 160, 161)—*?spherioidea*.
 Nieuwlandii (2: 171, 176)—*novae angliae*
 var. *Nieuwlandii*.
 novae-angliae (2: 172, 177)—*novae-*
 angliae.
 obesa (2: 160, 162)—*?spherioidea*.
 opima (2: 92, 93)—*ligulistylis*.
 perusta (2: 92, 93)—*ligulistylis*.

petiolata (2: 172, 176)—*spherioidea*.
 porrecta (2: 160, 162)—*spherioidea* (some
 type duplicates are *ligulistylis*).
 praecellens (2: 160, 161)—*?spherioidea*.
 praiceps (2: 92, 93)—*ligulistylis*.
 praesignis (2: 171, 175)—see discussion
 under *L. aspera*.
 praestans (2: 92, 93)—*ligulistylis*.
 propinqua (2: 160, 162)—*spherioidea*.
 ramea (2: 160, 161)—*spherioidea*.
 salutans (2: 171, 176)—*spherioidea* var.
 salutans.
 scalaris (2: 127)—*ligulistylis*.
 singularis (5: 39)—*ligulistylis*.
 strictissima (2: 172, 177)—*spherioidea*.
 subcorymbosa (2: 158)—*ligulistylis*.
 subcymosa (2: 172, 177)—*spherioidea*.
 superans (2: 171, 176)—*spherioidea*.
 supereminens (2: 92, 93)—*ligulistylis*.
 superscandens (2: 160, 161)—*spherioidea*.
 uniflora (3: 344)—*ligulistylis*.
 virgata (2: 172, 177)—*spherioidea*.
 virginiana (2: 172, 177)—*scariosa*.

DEPARTMENT OF BOTANY,
 UNIVERSITY OF WISCONSIN,
 MADISON, WISCONSIN.

Notes on the Cyperaceae of Saskatchewan II.¹

Carex

G. F. Ledingham and W. P. Fraser

This paper is based largely on a study of the collections in the herbarium of the University of Saskatchewan, and field observations extending over several years. The herbarium contains a number of valuable duplicates of the collections of A. J. Breitung of McKague, and of J. L. Bolton of the Swift Current Experiment Station. Most of the collections were made in the southern half of the province, the settled area, and did not extend farther north than 54° N. Lat. except in the Prince Albert National Park and the Montreal Lake region.

Raup (Jour. Arn. Arbor. 17:217-221, 1936) reports a number of collections from the Athabaska Lake region. The species reported from the Saskatchewan portion of this area are included. None of these collections has been examined by the authors. Species listed by Mackenzie in *North American Flora*, as occurring in this province, are also included.

Brief descriptive notes of the species have been given with the hope that they may be of value to amateur botanists interested in this genus. Mackenzie's monograph of the genus *Carex* (*North American Flora*, vol. 18) has been followed in the arrangement of the sections and species.

Section 1, *Capitatae*

1. *Carex capitata* L. Collected in damp grassy places at Methye River by J. M. Macoun (Cat. Can. Plts. pt. 5, p. 375. 1888). Subarctic and alpine. Greenland to Hudson Bay to Alaska.

Section 2, *Divisae*

2. *Carex Douglasii* Boott. Locally common in meadows and dry open prairies. Sometimes in hard-packed soil. Low; spikes aggregated in a single, large head; dioecious. Manitoba to British Columbia and southward.

3. *Carex Eleocharis* L. H. Bailey. Common in dry, sunny places of the prairie. Early flowering, low; rootstocks slender; head rather small; perigynia dark brown. Manitoba to Yukon and southward.

4. *Carex simulata* Mack. Rare. Swamp, Pike Lake (20 miles southwest of Saskatoon). Resembles *C. praegracilis* in general appearance, but rootstocks brown and more slender.

Saskatchewan to Washington and southward.

5. *Carex praegracilis* W. Boott. Abundant in meadows and wet, open places in the settled area. Rootstocks stout and dark brown or black; spikes aggregated but distinct. A very variable species.

Manitoba to Yukon and southward.

Section 3, *Intermediae*

6. *Carex Sartwellii* Dewey. Rather common in meadows and borders of sloughs and marshes. Clearwater River, Macoun (Raup). Rootstocks stout, brown; leaves rather broad; sheaths green-striate.

Ontario to British Columbia south to Illinois and Colorado.

¹ See Can. Field-Nat. 54:100, 1940 for I.

Section 4, *Arenariae*

7. *Carex foenea* Willd.—*C. siccata* Dewey Rhodora 40:325-329, 1938). Common in dry woods and open sandy places. Rootstocks long-creeping, clothed with brown, fibrillose scales; spikes in an oblong head, the whitish margin of the scales giving the heads a dry appearance.

Maine to Mackenzie and Washington south to Indiana and Nebraska.

Section 5, *Chordorrhizae*

8. *Carex chordorrhiza* L. Rare. Peat bogs at McKague (Breitung), Waskesiu, Lake Athabaska (Raup). Old culms of previous year prostrate, sending up erect branches from nodes or apex; spikes few in a head; perigynia shining brown.

Labrador to Keewatin, locally south to Maine and Iowa.

Section 6, *Bracteosae*

9. *Carex Hoodii* Boott. A western mountain species. Lake shore at Cypress Hills. Caespitose; spikes aggregated in a dense head on long slender culms; perigynia brown with green beaks and margins.

Saskatchewan to British Columbia to California.

10. *Carex Hookerana* Dewey. Probably not rare in open prairie depressions. Caespitose; culms slender, usually curved above; head slender, somewhat drooping.

Manitoba and North Dakota to Alberta.

Section 7, *Multiflorae*

11. *Carex vulpinoidea* Michx. Rare. Wet shores of Montreal Lake and a pond in P. A. Nat. Park. Dense clumps; culms stiff, erect; heads large and dense, greenish yellow when young, prickly appearance.

New Brunswick to British Columbia and southward.

Section 8, *Paniculatae*

12. *Carex diandra* Schrank. Common in swamps and on the marshy shores of non-alkaline lakes. Large, dense clumps; sheaths thin, ventrally dotted with brown; head little interrupted.

New Brunswick to Yukon south to Indiana and Colorado.

13. *Carex prairea* Dewey. Common in the settled area in bogs and along streams. Sheaths copper-colored above; head interrupted.

Quebec to Saskatchewan, southward to New Jersey and Nebraska.

Section 9, *Vulpinae*

14. *Carex stipata* Muhl. Occasional in wet places, chiefly northward. Caespitose; heads large, compound, prickly appearance.

Newfoundland to Alaska and southward.

15. *Carex alopecoidea* Tuckerman. Moist soil at McKague (Breitung). An eastern species not previously reported from Saskatchewan.

Quebec to Saskatchewan southward to New Jersey and Iowa.

Section 10, *Heleonastes*

16. *Carex disperma* Dewey. (*C. tenella* Schkuhr.) Common in boggy woods especially northward. A slender, weak, caespitose species; perigynia few, dark and shining when fully mature.

Newfoundland to Alaska and southward.

17. *Carex trisperma* Dewey. Eastern. Reported from Sask. by Mackenzie.

Labrador to Saskatchewan and southward.

18. *Carex tenuiflora* Wahl. Apparently rare. Bogs at Crooked River and Waskesiu; Lake Athabaska (Raup). Pale green; culms elongate, bearing 2-4 closely aggregated spikes.

New Brunswick to Yukon, southward to Maine and Minnesota.

19. *Carex liliacea* L. Muskeg, Cornwall Bay, Lake Athabaska (Raup). Saskatchewan to British Columbia and Yukon.

20. *Carex Heleonastes* L. Rare. Open bogs, McKague (Breitung), Waskesiu. Stems stiff and erect; resembles *C. interior* in general appearance. Ontario to Mackenzie and British Columbia.

21. *Carex brunnescens* (Pers.) Poir. var. *sphaerostachya* (Tuckerm.) Kukenth. (Rhodora 28; 163. 1926). Occasional in boggy woods northward. Lake Athabaska (Raup). In large tufts; culms slender, lax; spikes usually strongly separate. Newfoundland to New Jersey to Alaska and Washington.

22. *Carex canescens* L. var. *subloliacea* Laestad. Occasional in swamps and bogs in the northern areas. Lake Athabaska (Raup). Densely caespitose; leaves glaucous-green; culms erect.

Greenland to Alaska and southward.

Section 11, *Dioicae*

23. *Carex gynocrates* Wormsk. Common in wet mossy woods from Beaver Creek (Saskatoon) northward. Dioecious; culms slender, low, with solitary spike; brownish, reflexed perigynia; stolons slender.

New Brunswick to British Columbia.

Section 12, *Stellulatae*

24. *Carex interior* L. H. Bailey. Rather common in swamps. Caespitose; strict, wiry, culms; spikes 2-4, with reflexed or spreading perigynia, blades of leaves usually flat.

Labrador to British Columbia and southward.

25. *Carex sterilis* Willd. Swamps at Macdowall, Prince Albert and Waskesiu. Resembles *C. interior*; staminate flowers often in separate spikes; blades of leaves canaliculate or involute.

Newfoundland to Saskatchewan to Pennsylvania.

Section 13, *Deweyanae*

26. *Carex Deweyana* Schw. Common in dry woods and shaded places. Caespitose; culms usually weak and spreading; leaves light green, rather broad.

Newfoundland to Mackenzie to British Columbia and southward to Pennsylvania and Colorado.

Section 14, *Ovales*

27. *Carex festivella* Mack. At Cypress Hills and in the north. Rather common in moist ground. Large clumps; spikes aggregated in a dense head.

Manitoba and South Dakota to British Columbia and California.

28. *Carex pachystachya* Cham. Springy place in Cypress Hills. Resembles *C. festivella* in appearance. Not previously reported from Saskatchewan.

Saskatchewan to British Columbia southward to Wyoming and Colorado.

29. *C. praticola* Rydb. Common in moist places and open woods. Spikes usually forming a moniliform inflorescence, flexuous, slightly nodding.

Labrador to Yukon and southward.

30. *Carex pelasata* Dewey. Open woods and meadows at Cypress Hills. Inflorescence moniliform; perigynia large, concealed by scales.

Saskatchewan to British Columbia to Colorado.

31. *Carex Crawfordii* Fern. Not common. Moist places and sandy shores. McKague (Breitung), Meadow Lake, Montreal Lake. Spikes closely aggregated into a linear-oblong or oblong head; perigynia thin, lanceolate-subulate.

Newfoundland to British Columbia and locally southward.

32. *Carex scoparia* Schkuhr. Border of Lake Carnduff (T. N. Willing). Apparently rare. Resembles *C. Crawfordii* in appearance but larger and inflorescence sometimes moniliform; perigynia lanceolate or ovate-lanceolate.

Newfoundland to British Columbia and southward.

33. *Carex Bebbii* Olney. Rather common in moist places. Spikes subglobose, closely aggregated into an oblong head.

Newfoundland to British Columbia southward to New Jersey, Colorado and Wash.

34. *Carex tenera* Dewey. Occasional in prairie depressions and moist open woods. Culms slender; spikes usually in a moniliform inflorescence.

Quebec to Alberta.

35. *Carex brevior* (Dewey) Mack. Occasional. Moist open places from Saskatoon southward. Perigynia broadly ovate to orbicular.

Quebec and Maine to British Columbia and Texas.

36. *Carex Bicknellii* Britton. Reported in Saskatchewan by Mackenzie.

Maine to Saskatchewan to Arkansas.

37. *Carex cumulata* (Bailey) Mack. Reported by Mackenzie.

Nova Scotia and New Jersey to Saskatchewan.

38. *Carex cristatella* Britton. Moist, open shores of Pike Lake and a pond in P. A. Nat. Park. Spikes globose or subglobose in a dense oblong head; tips of achenes recurved.

Massachusetts to Saskatchewan southward to Virginia and Missouri.

39. *Carex xerantica* Bailey. Occasional in depressions of the open prairie, rather common in the south. Culms stiffly erect; inflorescence erect, elongate, dry chaffy appearance when mature.

Manitoba to Alberta to New Mexico.

40. *Carex adusta* Boott. Sandy soil in P. A. National Park. Culms stiffly erect; spikes aggregated into a heavy, erect, ovoid to linear head; lowermost bract usually well-developed.

Newfoundland and New York to Saskatchewan and Mack.

41. *Carex aenea* Fern. Occasional in sandy soil. Lake Athabaska (Raup). Culms tall, nodding; spikes in a flexuous, moniliform inflorescence.

Labrador to British Columbia.

42. *Carex athrostachya* Olney. Rather common in moist shaded ground. Bracts conspicuously exceeding head; narrow and long attenuate.

Saskatchewan to British Columbia and southward.

43. *Carex sychnocephala* Carey. Rather common in moist meadows and thickets. Extending northward to the western end of Lake Athabaska (Raup). Densely caespitose; bracts many times exceeding head, broad at base and enfolding it.

Ontario to Saskatchewan to Iowa.

Section 15, *Polytrichoideae*

44. *Carex leptalea* Wahl. Wet woods and shady, springy places, more common northward. Densely caespitose; culms slender, low; spike solitary.

Labrador to Alaska and southward.

Section 16, *Phyllostachyae*

45. *Carex Backii* Boott. Dry wooded banks. Cypress Hills, Waskesiu, McKague (Breitung). Caespitose; low; scales leaf-like, concealing and partly enveloping head. Quebec to New York to British Columbia.

46. *Carex saximontana* Mack. Dry wooded banks, Moose Jaw, Elbow and Saskatoon.

Resembles *C. Backii* but beaks of perigynia shorter and serrulate.
Manitoba to British Columbia to Nebraska.

Section 17, *Filifoliae*

47. *Carex filifolia* Nutt. Common on dry hillsides in the prairie region. Densely caespitose; leaves wiry, stiff, involute; spike solitary, whitish.
Texas to Manitoba to Yukon.

Section 18, *Obtusatae*

48. *Carex obtusata* Lilj. Common on dry, open prairie. Low; solitary spike; slender rootstock.
Yukon to Manitoba southward.

49. *Carex supina* Willd. Arctic. Lake Athabaska (Raup).
Greenland to Mack.

Section 19, *Montanae*

50. *Carex Peckii* Howe. Common in rich soil and leaf mold. Loosely caespitose; culms usually much exceeding leaves; perigynia hirsute.
Quebec to Yukon south to British Columbia and New York.

51. *Carex heliophila* Mack. Common in dry, open ground northward to Prince Albert and McKague. Reddish-brown tinged and strongly fibrillose at base; culms erect; leaves firm, attenuate. Closely related to *C. pennsylvanica*.
Manitoba to Alberta and southward.

52. *Carex deflexa* Hornem. Lake Athabaska (Raup).
Nova Scotia to Alaska and British Columbia.

53. *Carex Rossii* Boott. Common on dry banks. Clearwater River, Macoun (Raup). Low; caespitose; fertile culms vary much in length.
Michigan to Yukon to California.

54. *Carex tonsa* (Fern.) Bickn. (*C. umbellata* var. *tonsa* Fernald). Dry, sandy soil at Prince Albert. Noted by Richardson at Methye Portage (Raup). Very low plant; pistillate spikes on slender peduncles varying in length, often so short the spikes are hidden by the leaves.

Nova Scotia to Indiana to Alberta.

55. *Carex umbellata* Schukr. Reported from Saskatchewan by Mackenzie.
Newfoundland to British Columbia to Illinois.

Section 20, *Scirpinæ*

56. *Carex scirpoidea* Michx. Arctic and alpine. Lake Athabaska (Raup).
Greenland to Michigan to Alaska to Colorado.

57. *Carex scirpiformis* Mack.—*C. scirpoidea* var. *scirpiformis* (Mack) O'Neill and Duman (Rhodora 43:417, 1941). Common in wet meadows and bogs. Dioecious; culms slender, stiffly erect; spike usually solitary, narrow cylindrical.
Manitoba to Alberta south to North Dakota and Montana.

Section 21, *Digitatae*

58. *Carex concinna* R. Br. Occasional. Moist coniferous woods, McKague (Breitung), MacDowall, Prince Albert, L. Athabaska (Raup). Early; culms slender, leafy at base; perigynia strongly hirsute, greenish.
Newfoundland to Yukon to British Columbia locally southward.

59. *Carex Richardsonii* R. Br. Occasional in dry, sandy soil. L. Athabaska (Raup). Slender, curving culms, longer than leaves; bracts spathe-like, reddish brown with white margins.

New York and Ontario to British Columbia.

Section 22, *Rupestres*

60. *Carex glacialis* Mack. Arctic. L. Athabaska (Raup).
Newfoundland to Yukon.

Section 23, *Albae*

61. *Carex eburnea* Boott. Occasional on dry shaded banks. Caespitose; culms slender, erect; leaves fine, involute; perigynia blackish when fully mature.
Newfoundland to Mackenzie south to Nebraska and Pennsylvania.

Section 24, *Bicolores*

62. *Carex Garberi* Fern. var. *bifaria* Fern. (Rhodora 37:253-255. 1935). Bogs and wet places, McKague and Walwort (Breitung), Pike Lake, Waskesiu. Resembles *C. aurea* when immature.

Quebec to Maine to British Columbia.

63. *Carex aurea* Nutt. Common in moist open and shaded places. Perigynia orbicular, somewhat flattened, fleshy, orange or brownish when mature.

Newfoundland to British Columbia to Nebraska.

Section 25, *Paniccae*

64. *Carex livida* (Wahl.) Willd. Bogs at Dahltun (Breitung), Prince Albert, Pike Lake. Plant pale, greenish-glaucous including perigynia.

Newfoundland to Alaska to California.

65. *Carex tetanica* Schkuhr. In range according to Mackenzie. Abundant in Manitoba and westward (Macoun, Cat. Can. Plants).

Massachusetts to Alberta to Wisconsin.

66. *Carex Meadii* Dewey. "File Hills and Assiniboia" Qu'Appelle valley (Macoun, Cat. Can. Plants). Reported from Saskatchewan by Mackenzie.

New Jersey to Saskatchewan to Texas.

67. *Carex saltuensis* L. H. Bailey. (*C. vaginata* var. *allocaulis* Dewey). Rather common in boggy woods northward. Culms usually ascending, longer than leaves; spikes on slender peduncles; perigynia usually yellowish-brown with curved beak.

Newfoundland to Yukon to British Columbia and southward.

Section 26, *Laxiflorae*

68. *Carex plantaginea* Lam. Recorded from Saskatchewan by Mackenzie.

Quebec to Saskatchewan southward to North Carolina and Kentucky.

Section 27, *Granulares*

69. *Carex Haleana* Olney. Recorded by Mackenzie.

Quebec to Saskatchewan southward to Kansas and Virginia.

Section 28, *Sylvaticae*

70. *Carex assiniboinensis* W. Boott. Rare. Shaded banks at Moose Jaw and Lake Katepwa. Culms weak, slender; pistillate spikes on slender, drooping peduncles; perigynia hispid with very long, slender beaks.

Manitoba, Saskatchewan south to Wisconsin and Iowa.

Section 29, *Capillares*

71. *Carex capillaris* L. Common in wet shady places chiefly northward. Culms slender; pistillate spikes on very slender, drooping peduncles.

Greenland to Alaska southward to New Mexico and Maine.

Section 30, *Longirostres*

72. *Carex Sprengelii* Dewey. Common on wooded banks north to Saskatoon and McKague. Collected at Clearwater River by Macoun (Raup). Base of culms and stout

rootstock strongly brown, fibrillose; pistillate spikes pendulous on slender peduncles, body of perigynia rounded, very abruptly contracted into a slender beak.

New Brunswick to Alberta southward to Pennsylvania and Colorado.

Section 31, *Extensae*

73. *Carex viridula* Michx.—*C. Oederi* Retz. var. *pumila* (Cosson and Germ) Fern.—Bogs at Golburn (Breitung), Pike Lake, Prince Albert Nat. Park, Madge Lake, Clearwater River by Macoun (Raup). Culms erect; spikes crowded at summit; bracts leaf-like, conspicuous.

Newfoundland to Alaska to New Mexico.

Section 32, *Virescentes*

74. *Carex Torreyi* Tuckerm. (*C. abbreviata* Prescott). Occasional in low, partially shaded places. Culms erect; spikes clustered at top; perigynia finely and strongly ribbed, depressed and abruptly rounded at apex.

Manitoba to Alberta southward to Minnesota and South Dakota.

Section 33, *Hirtae*

75. *Carex Houghtonii* Torr. Rare. Damp gravelly soil at Prince Albert Nat. Park and Tallpines. Culms stout; stolons strongly developed; pistillate spikes stout; perigynia hispid, strongly many-ribbed.

Newfoundland to Saskatchewan to Minnesota and Maine.

76. *Carex lanuginosa* Michx.—*C. lasiocarpa* ssp. *lanuginosa* (Michx). Clausen and Wahl (Rhodora 41:481, 1939).—Common in wet places north to Prince Albert and McKague. Stolons long; perigynia densely hairy, abruptly beaked; beak strongly bidentate.

New Brunswick to British Columbia and southward.

77. *Carex lasiocarpa* Ehrh. Occasional in bogs and low marshy shores northward from Prince Albert and McKague. Resembles *C. lanuginosa* but leaf blades involute and very long attenuate; lowest bract strongly exceeding culm.

Newfoundland to British Columbia southward to Pennsylvania and Wash.

Section 34, *Limosae*

78. *Carex limosa* L. Rather common in bogs from Pike Lake and McKague northward. Low; culms slender; staminate spike stalked, erect; pistillate spikes on very slender peduncles, drooping.

Newfoundland to Yukon to California.

79. *Carex paupercula* Michx. Boggy woods and muskegs from Prince Albert to Crooked River and northward. Culms slender; pistillate spikes usually drooping on slender peduncles; the dark-colored cuspidate scales make the spikes conspicuous. The variety *irriqua* (Wahl.) Fern. is reported from Poplar Point on Lake Athabaska by Raup.

Newfoundland to Alaska southward to Pennsylvania and Colorado.

Section 35, *Atratae*

80. *Carex Parryana* Dewey. Occasional in low meadows and borders of bogs from Saskatoon and Wadena northward. Culms slender, stiff; spikes linear, erect, dark brown in color.

Manitoba and Alberta to Mack.

81. *Carex VahlII Schkuhr*, var. *inferalpina* (Wahl.) Fern. (Rhodora 35:414, 1933.) Rather rare. Wet coniferous woods, McKague (Breitung), Methye Portage by Macoun (Raup), Prince Albert Nat. Pk., Tallpines. Culms slender, much exceeding leaves; spikes closely aggregated; perigynia yellowish-white at first, becoming yellowish-brown.

Newfoundland to Alaska and southward.

82. *Carex Reynoldsii* Dewey. Rare. Mountain Meadow at Cypress Hills (Bolton). Conspicuous; pistillate spikes rather large, clustered, erect on slender peduncles.

Saskatchewan and British Columbia to Colorado and California.

83. *Carex atratifomis* Britton. Occasional. Moist ground in partial shade. McKague (Breitung), Tallpines, Montreal Lake, Green Hills, Prince Albert Nat. Park. Forming clumps; culms rather slender; pistillate spikes lateral, large, brown, nodding on slender peduncles.

Labrador to Yukon southward to Maine and Alberta.

84. *Carex Buxbaumii* Wahl. L. Athabaska (Raup).
Newfoundland to Alaska and southward.

Section 36, *Acutae*

85. *Carex lenticularis* Michx. L. Athabaska (R.S. Campbell). Newfoundland and Massachusetts to Mackenzie and Idaho.

86. *Carex aquatilis* Wahl. Very abundant in the north, in swampy places and marshy shores of lakes and rivers. Culms, tall, erect; leaves light-green or glaucous-green, long tapering; pistillate spikes narrow, erect; scales brown to purplish-black.

Labrador to Alaska and southward.

87. *Carex substricta* (Kukenth) Mack. Reported from the prairie provinces of Canada by MacKenzie. Not collected or recognized by the authors. All collections of this type have been placed in *C. aquatilis*.

Newfoundland to Washington and southward.

Section 37, *Pseudo-Cyperae*

88. *Carex hystricina* Muhl. Rare. Pike Lake, in wet, springy, shaded places. Macoun (Cat. Can. Plants) reports it as "not uncommon throughout the prairie regions north of Lat. 52° N." Pistillate spikes drooping on slender peduncles, bristly appearance from the long awned scales; perigynia green or greenish, straw-colored at maturity.

New Brunswick to Saskatchewan and Washington and southward.

89. *Carex Pseudo-Cyperus* L. Rare. Bog at McKague (Breitung). No other definite report of its occurrence in Saskatchewan has been found. Pistillate spikes, several, nodding on slender pedicels; perigynia at base of spikes reflexed.

Newfoundland to Saskatchewan and southward.

Section 38, *Paludosae*

90. *Carex lacustris* Willd. Marshy shores of lakes and sloughs, McKague (Breitung), Waskesiu, Montreal Lake. Culms tall; leaves well-developed, broad, dark-green; perigynia large, green, many-ribbed, tapering into a smooth, short, bidentate beak.

Nova Scotia to Saskatchewan to Iowa.

91. *Carex laeviconica* Dewey. Rare. Low meadows, Moose Jaw. Resembles *C. atherodes* but lacks hairs on the leaf sheaths and teeth on the perigynia are only half as long.

Saskatchewan to Montana, Illinois, Missouri, Kansas.

92. *Carex atherodes* Spreng.—*C. trichocarpa* Muhl. var. *aristata* (R. Br.) Bailey.—Abundant around sloughs and lakes and along streams. Culms, tall, stout, sharply triangular; sheaths usually soft hairy; perigynia strongly many-ribbed, tapering into a strongly bidentate beak, teeth long and slender, usually widely spreading.

Ontario to Yukon south to Colorado, Indiana and New York.

Section 39, *Vesicariae*

93. *Carex physocarpa* Presl. Arctic and alpine. L. Athabaska (Raup).
Pribolof Islands to Yukon to Colorado.

94. *Carex Racana* Boott. Type specimen collected at Methye Portage by Richardson (Raup). Otherwise unknown in Saskatchewan.

Maine to Quebec to Saskatchewan.

95. *Carex vesicaria* L. Apparently very rare. Only collection at Trossachs in southern Saskatchewan by Bolton. Perigynia gradually beaked; lower sheaths fragile, becoming filamentose. Rootstocks with long horizontal stolons.

Newfoundland to British Columbia and southward.

96. *Carex rostrata* Stokes (*C. utriculata* Boott.) Abundant around sloughs, lakes along creeks and in wet places. Perigynia when mature abruptly beaked; lower ones not fragile, becoming filamentose; rootstocks with long horizontal stolons

Greenland to Alaska and southward.

97. *Carex retrorsa* Schw. Occasional in swampy shaded places. Spikes large, stout; perigynia much-inflated, reflexed below; bracts leathery.

Nova Scotia to British Columbia to Colorado.

98. *Carex oligosperma* Michx. "Peat bogs Methye Portage Lat. 57° where it is in abundance" (Macoun, Cat. Can. Plants). "Common on sandy pond margins on the south side of Lake Athabaska" (Raup).

Labrador to Mackenzie southward to Indiana and Massachusetts.

CHANGE OF NAMES

A recent paper by Fernald, *Rhodora* 44:281-331, (1942) indicates the following change of names in this list:

77. *Carex lasiocarpa* Ehrh. to the variety *Carex lasiocarpa* Ehrh. var. *americana* Fern.

81. *Carex Vahlü* Schkuhr var. *inferalpina* Fern. to *Carex media* R. Br. (*Carex angarae* Steud.)

86. *Carex substricta* Kuentz. to *Carex aquatilis* Wahl. var. *altior* (Rydb.) Fern. The range is more southern than Saskatchewan.

96. *Carex rostrata* Stokes to *Carex inflata* Huds., the valid name. The species is rare and northern. Collections from Lake Athabaska (Sask.) are assigned to the species. The very common plant belongs to the variety *Carex inflata* Huds. var. *utriculata* (Boott) Druce.

JUNIOR COLLEGE, MOOSE JAW,
UNIVERSITY OF SASKATCHEWAN, SASKATOON.

New Species of Oscillatoriaceae

Francis Drouet

Specimens cited here are all to be found in the Cryptogamic Herbarium of Field Museum or in the personal herbarium of the writer.

Schizothrix Macbridei, sp. nov.

Stratum tenue pannosum fragilissimum griseo-aerugineum vel decoloratum, filis primum tortilibus unitrichomatiferis inter alias myxophyceas crescentibus, aetate provecta pluritrichomatiferis atque copiose fasciculato-ramosis, ramis in fasciculos breves decumbentes tortis; vaginis arctis tenuibus hyalinis demum luteolis, ambitu erosis, chlorozincico iodurato laete caerulescentibus; trichomatibus pallide aerugineis, $2\ \mu$ ad $3\ \mu$ crassis, cylindricis, ad genicula constrictis, ad apices longe et sensim attenuatis et acuminatis; articulis subquadratis vel diametro plus minusve longioribus vel brevioribus, protoplasmate non aut vix granuloso, dissepimentis pellucidis; cellula apicali longe et fere acutissime conica.

Growing as thin crusts on silt in slight depressions in barren ground. It is a member of Gomont's section Chromosiphon, to be placed near *S. Lamyi* Gom. This new species is named in honor of Mr. J. Francis Macbride of Field Museum. Among numerous specimens seen, the following are cited as representative.

NEBRASKA: 13 miles west of Hastings, Adams county, *W. Kiener 13036*, Sept. 1942. COLORADO: Mount Blanca, Costilla county, *Macbride 7517*, Sept. 1942; east of Lajunta, Otero county, *Drouet, D. Richards, & J. Rubinstein 4005*, Sept. 1941. ARIZONA: near Winslow, Navajo county, *Macbride 7538*, Sept. 1942. CALIFORNIA: black lava-flows east of Bagdad, San Bernardino county, *Drouet & Macbride 4636*, Oct. 1941 (TYPE in Cryptogamic Herbarium of Field Museum); near Hopkins Well, Riverside county, *Drouet & Macbride 4728*, Oct. 1941; 2 miles west of Coyote Well, Imperial county, *Drouet & Macbride 4791*, Oct. 1941. SONORA: near Rio de Sonora, Hermosillo, *Drouet & Richards 2868*, Nov. 1939.

Schizothrix Stricklandii, sp. nov.

Stratum expansum pannosum, olivaceum vel aerugineum vel nigrum, filis longis subrectis robustis, inferne intricatis, superne ramosis saepe in fasciculos breves erectos contortis; vaginis hyalinis primum tenuibus, aetate provecta incrassatis et lamellosis, ambitu erosis, chlorozincico iodurato laete caerulescentibus; trichomatibus aerugineis vel olivaceis, $4\ \mu$ ad $6\ \mu$ crassis, ad genicula non aut vix constrictis, ad apices non aut paullo attenuatis; cellulis quadratis vel diametro brevioribus (nonnumquam longioribus), dissepimentis praecipue conspicuis, protoplasmate granuloso; cellula apicali brevi et truncato-conica, membrana superna incrassata et plus minusve depresso-conica.

An often encountered species growing in pannose strata in barren ground of fields and open woods throughout temperate North America. It is a member of Gomont's section *Symplocastrum*. Many of the specimens placed here have been distributed to various herbaria under the name *S. Friesii* Gom. *S. Stricklandii* occupies habitats kept not so constantly wet as those inhabited by *S. Friesii*; its filaments are in general longer and its cells shorter than those of the latter species. Its most distinctive feature is the thickened outer membrane of the apical cell. It is named for Mr. J. C. Strickland, Jr., of the University of Virginia. Among the many specimens at hand the following are chosen as representatives of the species.

NEW JERSEY: pasture-land between Myrtle Grove and Pisgah, Sussex county, Drouet & H. F. Herpers 3675, July 1941. PENNSYLVANIA: Cresheim creek, Fairmount park, Philadelphia, Drouet & C. Hodge 3886, July 1941. MARYLAND: Plummers island west of Cabin John, Montgomery county, Drouet, E. P. Killip, & J. R. Swallen 3902, 3916, July 1941. DISTRICT OF COLUMBIA: near Chesapeake & Ohio canal, M. A. Fitch & C. T. Velasquez 68, Sept. 1939. VIRGINIA: south of Chilhowie, Smyth county, P. R. Burch & J. C. Strickland 1076, August 1941. NORTH CAROLINA: Chapel Hill, Orange county, A. W. Evans, Sept. 1937; at Harbison lake, Highlands, Macon county, H. C. Bold H311, July 1939. OHIO: gravel pit at fairgrounds, Cincinnati, W. A. Daily 186, 187, Oct. 1939. KENTUCKY: at the lagoon, Ludlow, Kenton county, Daily 239, Nov. 1939. INDIANA: by the Whitewater river, Richmond, Wayne county, L. J. King 21, August 1940. ILLINOIS: Willow Springs, Cook county, P. C. Standley, J. A. Steyermark & Drouet 2432, Oct. 1938. MINNESOTA: Big Thunder lake south of Remer, Cass county, D. Richards 1401, August 1942. MISSOURI: near Ashland arboretum in Callaway county, W. B. Drew 240H, August 1940. NEBRASKA: north branch of Middle creek, Seward county, W. Kiener 13003a, August 1942. CALIFORNIA: Weaverville, Trinity county, Drouet & Richards 4261, 4722, 4275, 4277 (TYPE in the Cryptogamic Herbarium of Field Museum), 4278, Sept. 1941; along Colorado river 10 miles south of Vidal in Riverside county, Drouet & Macbride 4654, Oct. 1941. GUATEMALA: near La Fragua, Dept. Zacapa, P. C. Standley 74772, Oct. 1940.

Schizothrix californica, sp. nov.

Stratum pannosum fragile, aerugineum vel decoloratum, filis primum unitrichomatiferis tortilibus inter varias myxophyceas crescentibus, demum basin pluritrichomatiferis rectis et supra fastigiato-ramosis, ramis longis tortilibus trichomata praecipuius solitaria includentibus; vaginis hyalinis arctis demum crassioribus atque obscure lamellosis, ambitu erosis, chlorozincico iodurato caerulescentibus; trichomatibus pallide aerugineis vel viridi-aerugineis, 2 μ ad 5 μ crassis, cylindricis, ad genicula non constrictis, ad apices brevi-attenuatis; articulis quadratis vel diametro usque duplo longioribus, protoplasma sparse tenui-granuloso, dissepimentis pellucidis; cellula apicali truncato-conica.

Growing with other algae in crusts on barren ground, commonly associated with *Microcoleus vaginatus* Gom. Where sparsely represented in mixtures with other algae, the filaments contain habitually solitary trichomes and have the general aspect of those of a tenuous strain of *Symploca Muscorum* Gom. *Schizothrix californica* belongs in Gomant's section *Symplocastrum*; the trichomes resemble somewhat those of *S. Friesii* Gom. but are smaller than the latter and are unconstricted at the cross-walls. Except in the basal parts of

the older filaments the sheaths are thin and almost lyngbyoid. Representative specimens among the many at hand are the following.

MISSOURI: old field south of Boydsville, Callaway county, *W. B. Drew* 840A, August 1940. NEBRASKA: bank of Platte river, Ogallala, Keith county, *W. Kiener* 10686, August 1941; bank of Salt creek, Lincoln, *G. H. Giles*, May 1938. COLORADO: 20 miles northeast of Canon City, Fremont county, *Drouet & A. Cohen* 4984, July 1942. NEW MEXICO: plain west of Las Vegas, San Miguel county, *Drouet & D. Richards* 2567, Oct. 1939; upland plain, Shiprock, San Juan county, *J. F. Macbride* 7550, Sept. 1942. CALIFORNIA: Hinkley station, San Bernardino county, *Drouet & Macbride* 4563, Oct. 1941; in scrub-forest 2 miles southeast of Palm Springs, Riverside county, *Drouet & Macbride* 4746, Oct. 1941 (TYPE in Cryptogamic Herbarium of Field Museum).

Schizothrix Dailyi, sp. nov.

Fila inter alias myxophyceas in stratum pulvinatum calce induratum crescentia, longa recta plus minusve rigida, inferne trunciformia, superne laciniato-divisa, ramis longis rectis parallelis; vaginis hyalinis, inferne incrassatis et parce lamellosis, superne tenuibus et levibus, chlorozincico iodurato laete caerulescentibus; trichomatibus pallide aerugineis vel olivaceis, $3\ \mu$ ad $4\ \mu$ crassis, ad genicula non constrictis, ad apices sensim attenuatis et quasi-truncatis; articulis praecipuius $1\frac{1}{2}$ -plo longioribus, haud raro brevioribus vel longioribus, protoplasmate sparse grosse-granuloso, dissepimentis saepe granulatis; cellula apicali fere truncato-conica, membrana superna rotundata et incrassata.

Mixed with other algae in pulvinate calcified strata in seepage on limestone. *S. Dailyi* belongs in Gomont's section *Inactis* near *S. lacustris* Gom.; it can easily be distinguished from the latter by its more robust trichomes which appear almost capitate at the apices. It is named for Mr. William A. Daily of the Herbarium of Butler University.

The one collection is from INDIANA: in quarry at St. Paul, Shelby county, *F. K. & W. A. Daily* 881, August 1941 (TYPE in Cryptogamic Herbarium of Field Museum).

Symploca Kieneri, sp. nov.

Stratum extensum pannosum nigrum vel olivaceum vel aerugineum, filis longis gracilibus, inferne tortilibus atque intertextis, superne raro in fasciculos erectos vel repentes paralleliter coadnatis; vaginis hyalinis crassis obscure lamellosis ambitu erosis, chlorozincico iodurato aegre (aut aetate provecta non) caerulescentibus; trichomatibus aerugineis vel viridibus vel luteolis, $4\ \mu$ ad $10\ \mu$ crassis, ad genicula paullo constrictis, ad apices sensim attenuatis; cellulis quadratis usque ad duplo longioribus, protoplasmate sparse grosse-granuloso, dissepimentis conspicuis haud granulatis; cellula apicali rotundata vel truncato-conica, membrana superna evidenter incrassata.

In barren depressions in sand. *S. Kieneri* is similar in general appearance to *S. Muscorum* Gom. where viewed under low magnifications; but the sheaths become thicker than do those of the latter species, and the trichomes here are distinctly constricted at the cross-walls. This new species, unlike *S. Muscorum*, occupies habitats which remain wet for very brief periods after rains. It is named for Dr. Walter Kiener of the Conservation and Survey Division, Uni-

versity of Nebraska. The specimens cited here have been distributed to other herbaria under the names *S. Muscorum*, *Porphyrosiphon fuscus* Gom., and *Schizothrix californica* Drouet.

FLORIDA: near Eustis, Lake county, *W. R. Maxon* 10952, Jan. 1938; Bonita Beach, Lee county, *P. C. Standley* 73219, March 1940; Naples and Marco island, Collier county, *Standley* 73381, 73409, March 1940. INDIANA: between Miller and Tremont, Lake county, *P. D. Voth & Drouet* 2358, Sept. 1938. ILLINOIS: Dunes state park, Lake county, *Drouet, Standley, & J. A. Steyermark* 3501 (TYPE in Cryptogamic Herbarium of Field Museum), 3525, June 1940. NEBRASKA: southwestern Hayes county, *W. Kiener* 10823, August 1941. CALIFORNIA: Santa Ana wash north of Redlands, San Bernardino county, *G. J. Hollenberg* 3165, March 1941. SONORA: Cerro de la Campana, Hermosillo, *Drouet, D. Richards, & L. D. Alvarado* 2785, Nov. 1939; Cabo Arco and Punta San Pedro, Guaymas, *Drouet & Richards* 3337, 3379a, 3380, Dec. 1939; southeastern shore of bay, Empalme, *Drouet & Richards* 3437, Dec. 1939.

FIELD MUSEUM OF NATURAL HISTORY,
CHICAGO, ILL.

The Ecological Anatomy of Ponderosa Pine Needles

Austin E. Helmers

This paper is the result of a study of the needle anatomy of ponderosa pine as influenced by differences in position on the tree as well as from trees growing in different environments.

Although there is an extensive literature on the ecological anatomy of leaves, a very small proportion of it is concerned with conifer needles. The present study also differs from the majority of the researches in this field in that the data were obtained in such a manner as to permit their biometric analysis.

The writer wishes to acknowledge with sincere appreciation the help of Dr. R. F. Daubenmire who suggested the problem and under whose direction the work was carried out, and Dr. H. K. Schultz for his suggestions concerning statistical methods.

Methods

The needle samples used in this study were collected from trees within a small area on Paradise Ridge, an outlying foothill at the western edge of the Bitterroot Mountains, located approximately four miles south and one-fourth miles east of Moscow, Idaho. A small area was sampled in order to confine the habitat variations to certain pairs of contrasted conditions which were of special interest. With such a restricted sample area there is little possibility but that the individual trees are of the same ecotype, and that the air temperature and precipitation are relatively uniform.

The extremes in habitats sampled are not of the greatest range possible on the ridge. For example, wind deformed trees on the summit were compared with symmetrical trees a short distance down the leeward slope. Much greater contrast could have been obtained by comparing ridgetop trees with trees on the northwest slope several miles distant, but in view of deeper soil, higher soil moisture content, greater snow accumulation, and cooler air temperatures in that location, many more factors other than exposure to desiccating winds might have influenced needle structure if comparative collections had been taken from there. Furthermore, the possibility of encountering a different ecotype would have increased.

The ridge from which the collections were made lies in the ecotone between the ponderosa pine (*Pinus ponderosa* Laws.) zone of the timbered foothills to the east and the fescue-wheatgrass (*Festuca idahoensis*-*Agropyron spicatum*) association of the Palouse prairie to the west. The trees grow in a savanna-like formation in the area studied.

Frequent outcropping of the parent rock show that the soil here is in no place very deep. Because of its thinness and coarse texture the soil on this ridge has a tendency to be droughty.

Needles were collected with a view to studying anatomical modifications due to (1) the effects of shade, (2) the effects of direction of exposure on the tree, (3) the effects of extreme exposure to wind, (4) the effects of height of insertion on the tree, and (5) the effects of age of tree.

Collections made to study the effects of 1, 2, and 3 above were made from the bases of the crown; samples used to study the effects of age were taken from the leaders of old and young trees. The young trees sampled were about one meter tall; all others were fairly mature trees about 4 dm. d.b.h. and 12 meters tall. The collections were made on October 2, 1941, using only needles formed the preceding year (1940) except for those collected to study the effects of age which were of 1941 origin.

Ten fascicles of needles were taken from each of three trees selected to represent a particular type of material. One needle was taken from each of these 3-needled fascicles and the ten homologous needles so obtained bound together. A segment 16 mm. long was removed near the center of each bundle for embedding and sectioning in collodion. Stomatal counts were made on the remaining portions of the needles adjacent to the segments preserved for sectioning, i.e., near the center of the needle. Stomata were counted on a band one millimeter wide extending completely around each needle. A glass microscope slide with two parallel lines of asphaltum one millimeter apart was used as a mask to delimit the width of the band. It was discovered that rubbing the surface of a fresh needle with the fingers removed a grayish surface film and made the whitish stomata easy to count using a 40x binocular microscope.

The sectioned material, after being stained and mounted, was measured with particular reference to the following characteristics which were selected because they could be readily measured and subjected to statistical analyses:

1. Depth of the outer stomatal chamber.
2. Thickness of cuticle.
3. Thickness of epidermis.
4. Thickness of hypodermis.
5. Cross-section area of needle.
6. Ratio of cross-section area of xylem to cross-section area of needle.
7. Ratio of cross-section area of xylem rays to cross-section area of xylem.
8. Ratio of cross-section area of xylem rays to cross-section area of stelar tissues.
9. Ratio of stelar to non-stelar tissues.
10. Number of stomata per unit area.
11. Amount of xylem per stoma.
12. Number of resin canals per needle.
13. Number of rows of stomata per needle.

Wherever the average of measurements (expressed in microns) of any of these characteristics differed between two contrasted sets of material, the "t-test" (Snedecor, 1940, p. 57) was used to evaluate the relative significance of the difference. In all tables the asterisks indicate the relative significances of the differences between means. A difference significant at the five per cent level (indicated by *) means that the odds are 19-1 that the difference between the two means tested is not merely due to chance. Similarly, a highly significant difference (**) for the one per cent level) indicates odds of 99-1. In cases

of nonsignificance (as shown by the absence of asterisks) the differences in measurements may be due to errors of random sampling.

Depth of the outer stomatal chamber.—The guard cells of the needles of *Pinus ponderosa* are sunken below the level of the other epidermal cells, so that the accessory cells form a cup-shaped depression or chamber immediately above the stoma. The distance from the level at which the two guard cells are closest together, to the distal limits of the stomatal chamber was measured and designated as the depth of the outer stomatal chamber. Three stomata from each of the ten needles in a sample were measured in this manner. The stomata chosen for measurement were obtained by random selection, except that only median cross-sections were used. Since near their ends the guard cells are triangular in shape and near the middle somewhat drop-shaped, the difference in shape provides a good criterion by which the median cross-section can be selected.

Thickness of cuticle.—On each of the ten needles in a collection the thickness of the cuticle was measured at three points equally spaced along the outer convex side of the needle. The three measurements from each needle were averaged and the result treated as one measurement in the statistical analyses.

Thickness of epidermis.—The epidermal layer varies considerably in thickness at different places on the same needle, becoming thinner adjacent to stomata. On each of ten needles per tree in a given habitat three measurements of thickness were made and averaged. The location of each point measured on the needle cross-sections was predetermined except for slight adjustments made to obtain the measurements at a point midway between adjacent stomata.

Thickness of hypodermis.—In determining the thickness of the hypodermis, four measurements from the outer convex surface were taken from each of the ten needles in each collection. As in the case of the epidermis, the locations of the points at which measurements were taken were determined mechanically and exceptions were made only when the position of a measurement coincided with a stoma.

Cross-section area of needles and tissues.—All cross-section area measurements were obtained by the use of a polar planimeter on camera lucida drawings of the structures. Xylem rays are generally uniseriate, but in a few instances xylem rays more than one cell in thickness were observed.

Ratios.—All ratios represent the quotient of the larger area divided by the smaller, i.e., cross-section area of needle/cross-section area of xylem, cross-section area of xylem/cross-section area of xylem rays, cross-section area of stelar tissues/cross-section area of xylem rays, and cross-section area of tissues outside the endodermis (non-stelar tissues)/cross-section area of tissues within the endodermis (stelar tissues). Unfortunately, with the technique employed it was not possible to relate stomatal frequency of each needle to the cross-section area of that particular needle, so that only means and the differences between the means could be used in this phase of the study.

Results

Effects of shade.—All of the following anatomical features showed a highly significant greater development in the sun needles as compared to shade needles (Table 1): depth of outer stomatal chamber, thickness of cuticle, thickness of epidermis, cross-section area of needles, greater proportion of xylem in the needle, larger stele in proportion to non-vascular tissue, greater number of stomata per unit area, greater number of resin canals per needle, greater number of rows of stomata per needle.

TABLE 1. Analysis of data on the effects of shade on needle structure.

Attribute	Series	Means with Standard Deviations	Diff. between Means with St'd. Errors *	Least Significant Mean Difference ^b	
				5%	1%
Depth of Outer Stomatal Chamber	Sun	24.29 ± 2.01	1.93 ± 0.280**	0.55	0.72
	Shade	22.36 ± 1.74			
Thickness of Cuticle	Sun	2.04 ± 0.32	0.32 ± 0.045**	0.09	0.12
	Shade	1.72 ± 0.29			
Thickness of Epidermis	Sun	12.89 ± 1.34	2.00 ± 0.304**	0.61	0.81
	Shade	10.89 ± 1.00			
Thickness of Hypodermis	Sun	24.77 ± 3.10	0.15 ± 2.836	5.67	7.54
	Shade	24.92 ± 3.81			
Cross-section Area of Needles in 0.1 mm. ²	Sun	11.74 ± 3.24	4.71 ± 0.605**	1.21	1.61
	Shade	7.03 ± 0.69			
Ratio: Area of Needle Area of Xylem	Sun	27.25 ± 9.33	7.69 ± 2.495**	4.99	6.64
	Shade	44.93 ± 9.99			
Ratio: Area of Xylem Area of Xylem Rays	Sun	5.44 ± 0.90	0.40 ± 0.262	0.52	0.70
	Shade	5.84 ± 1.23			
Ratio: Area of Stele Area of Xylem Rays	Sun	57.99 ± 17.92	8.42 ± 5.66	11.13	14.80
	Shade	66.41 ± 24.76			
Ratio: Area of Non-Stelar Tissues Area of Stele	Sun	2.53 ± 0.28	0.46 ± 0.063**	0.13	0.17
	Shade	2.99 ± 0.20			
Number of Stomata	Sun	229.8 ± 44.02	85.0 ± 8.328**	16.7	22.2
	Shade	144.8 ± 11.93			
Amount of Xylem in 0.00001 mm. ² per Stoma	Sun	15.16	4.05		
	Shade	11.11			
Number of Resin Canals	Sun	4.1 ± 1.94	1.1 ± 0.394**	0.8	1.0
	Shade	3.0 ± 0.93			
Number of Rows of Stomata	Sun	24.7 ± 4.74	8.9 ± 0.896**	1.79	2.38
	Shade	15.8 ± 1.29			

a In this column, throughout all 5 tables, a double asterisk indicates significance to at least the 1% level, a single asterisk to the 5% level, and the absence of either designation indicates nonsignificance.

b Calculations based on tables given by Snedecor (1940), p. 58.

The average thickness of the hypodermis showed the opposite tendency, being greater in the shade needles. However, this difference was small and nonsignificant.

Nonsignificant differences between needles in the sun as compared to needles in the shade were noted in regard to the proportion of cross-section area of xylem rays to cross-section area of xylem, and to the proportion of cross-section area of xylem rays to cross-section area of stelar tissues.

The significance of the greater amount of xylem per stomata in sun needles as compared to shade needles could not be determined for reasons stated previously.

The above results are in agreement with the majority of the previously published researches in which sun and shade or light effects were considered. Warming (1909, pp. 19-20) and Skipper (1922) found deeper stomata on sun leaves as compared with shade leaves, and according to Pick (1882), Stahl (1883), Dufour (1887), Chrysler (1904), and Harshberger (1908 and 1909), bright light also depresses stomata below the surface of the leaf.

In general, other investigators likewise have found the leaves of sun plants to have a thicker cuticle than leaves of shade plants (Dufour, 1887; Grevillius, 1897; Bergen, 1904; Clements, 1905; Harshberger, 1908 and 1909; Skipper, 1922; Pool, 1923; Cannon, 1924, p. 105; McDougall and Penfound, 1928; Büsgen and Münch, 1929, p. 226; Cain and Miller, 1933; and Duncan, 1933).

The results of the present study bear out the observations of Warming (1909, pp. 19-20), Pool (1923) and McDougall and Penfound (1928) who noted a thicker epidermis or a heavier epidermal wall on sun leaves as compared to shade leaves. The thickness of the epidermis has been found to increase in many cases with increasing intensity of light by Pick (1882), Stahl (1883), Dufour (1887), Grevillius (1897), Harshberger (1908), Hayden (1919), Skipper (1922), Bright (1928), and Whitfield (1933). On leaves of plants growing in the open Grevillius (1897), Lippmaa (1929), Cain and Miller (1933), and Shank (1938) found a thicker epidermis as compared to leaves of woodland plants.

Although the difference is not statistically significant, the greater average thickness of the hypodermis in shade leaves as compared to sun leaves is at variance with the results of most writers. While not specifically considering sun and shade environments, most investigators have observed a greater development of hypodermis under conditions of increased light* (Pick, 1882; Stahl, 1883; Dufour, 1887; Kearney, 1900; Schimper, 1903, pp. 4-7; Boodle, 1904; Harshberger, 1909; Warming, 1909, pp. 19-20; Büsgen and Münch, 1929, p. 226; and Cain and Miller, 1933).

To the extent that a comparison between broad leaves and needles can be made, the writer's results are in agreement with those of Dufour (1887), Haberlandt (1914, p. 295), Pool (1923), and Büsgen and Münch (1929, p. 225) who found that sun leaves were thicker than shade leaves. In connection with light intensity, Pick (1882) found that sun leaves and shade leaves had about equal surface areas but the thickness of the former was greater, and Clements and Long (1935) found that leaves became thinner with decreasing light intensity.

The present results are similar to those of Larsen (1927) who, in comparing different species of conifers representing different degrees of tolerance of shade, found that the proportion of xylem to the remainder of the leaf was larger in light-demanding species than in shade-enduring species. Alexsandrov

* Throughout this paper the writer has tried to preserve, where possible, a distinction between light *per se* and the contrasting complex of environmental factors which are implied by the expression "sun and shade."

and Dzharidze (1934) expressed the functional ability of the water conducting system of petioles as a ratio between the cross-section area of xylem and area of leaf blade. They found this ratio to be highest in sun plants and lowest in shade plants.

The results of studies by Bergen (1904), Hesselman (1904), Sampson and Allen (1909), Rea (1921), Skipper (1922), Bahgat (1923), Büsgen and Münch (1929, p. 225), Reed and Hirano (1931), and Whitfield (1933) are similar to those of the writer in that species of sun plants and sun leaves were found to have a greater density of stomata per unit leaf area than shade plants and shade leaves, respectively. On the cotyledonary leaves of certain tree seedlings, Schramm (1912) found the number of stomata per unit area to be higher on shade leaves than on sun leaves, but in one case at least he found the reverse to be true. On the leaves of mature trees and shrubs he found more stomata on sun leaves than on shade leaves.

The writer's results are comparable in another respect to those of Larsen (1927) who, in studying different species of conifers as representing different degrees of tolerance to shade, found that light-demanding species had a larger area of xylem per stoma than did the shade-enduring species.

The greater stomatal frequency on sun leaves is in accord with the findings of Clements and Long (1935) who observed that the major correlation in stomatal frequency was with light intensity, more stomata being found under conditions of increased light intensity. Reed and Hirano (1931) also found stomatal density to increase with light intensity.

Effects of direction of exposure.—Since the needles collected for studying the effects of direction of exposure could be compared by individual trees, i.e., northwest side of a tree with the southeast side of the same tree, the data were analyzed by trees in order to observe the degree of variation between them. It should be pointed out that in connection with these data as presented in table 2, more significance can be attached to individual comparisons (trees I, II, and III) than to the grouped comparisons because of the inherent variability among trees.

Comparisons between the northwest* and southeast sides of a tree show that reasonable confidence can be placed only in the differences in the thickness of the cuticle, which proved to be thicker on the needles from the southeast sides of the trees to a highly significant degree.

Although needles on the southeast sides of the trees differ significantly from the needles on the northwest sides in the attributes listed below, several irregularities between the sides of individual trees cast some doubt upon the calculated degree of significance of the entire group: greater depth of the outer stomatal chamber, larger cross-section area of needles, and larger proportion of cross-section area of xylem rays to cross-section area of xylem.

* Ostensibly more sheltered than due north since the trees were on the eastern side of a ridge extending northeast-southwest.

TABLE 2. Analysis of data on the effects of direction of exposure on needle structure.

Attribute	Tree No.	Series	Means with Standard Deviations	Diff. between Means with St'd. Errors	Least Significant Mean Difference	
					5%	1%
Depth of Outer Stomatal Chamber	I	NW	22.75 \pm 1.32	0.86 \pm 0.355*	0.714	0.944
		SE	23.61 \pm 1.43			
	II	NW	22.74 \pm 1.04	2.99 \pm 0.403**	0.81	1.07
		SE	25.73 \pm 1.86			
	III	NW	25.46 \pm 1.46	1.91 \pm 0.426**	0.85	1.13
		SE	23.55 \pm 1.82			
Thickness of Cuticle	I	NW	23.65 \pm 2.01	0.64 \pm 0.299*	0.59	0.78
		SE	24.29 \pm 2.01			
	II	NW	1.66 \pm 0.20	0.30 \pm 0.064**	0.13	0.17
		SE	1.96 \pm 0.28			
	III	NW	1.38 \pm 0.21	0.65 \pm 0.066**	0.13	0.18
		SE	2.03 \pm 0.29			
Thickness of Epidermis	I	NW	1.92 \pm 0.17	0.20 \pm 0.079*	0.16	0.21
		SE	2.12 \pm 0.40			
	II	NW	1.65 \pm 0.30	0.39 \pm 0.046**	0.09	0.12
		SE	2.04 \pm 0.32			
	III	NW	13.25 \pm 0.82	1.66 \pm 0.328**	0.69	0.94
		SE	11.59 \pm 0.84			
Thickness of Hypodermis	I	NW	11.49 \pm 0.64	2.89 \pm 0.289**	0.61	0.83
		SE	14.38 \pm 0.65			
	II	NW	14.44 \pm 0.48	1.74 \pm 0.334**	0.70	0.96
		SE	12.70 \pm 0.80			
	III	NW	13.06 \pm 1.37	0.17 \pm 0.350	0.70	0.93
		SE	12.89 \pm 1.34			
Cross-section Area of Needles in 0.1 mm. ²	I	NW	26.82 \pm 2.24	1.88 \pm 1.176	2.47	3.38
		SE	24.94 \pm 2.90			
	II	NW	25.66 \pm 2.00	0.72 \pm 1.133	2.38	3.26
		SE	24.94 \pm 2.97			
	III	NW	24.25 \pm 1.97	0.19 \pm 1.324	2.78	3.81
		SE	24.44 \pm 3.70			
Ratio: Area of Needle Area of Xylem	I	NW	25.58 \pm 2.30	0.81 \pm 0.497	0.99	1.32
		SE	24.77 \pm 3.10			
	II	NW	10.00 \pm 0.68	2.30 \pm 0.357**	0.75	1.03
		SE	7.70 \pm 0.80			
	III	NW	6.77 \pm 0.44	7.82 \pm 0.497**	1.04	1.43
		SE	14.59 \pm 1.51			
Ratio: Area of Needle Area of Xylem	I	NW	11.96 \pm 0.68	0.97 \pm 0.480	1.01	1.38
		SE	12.93 \pm 1.36			
	II	NW	9.58 \pm 2.25	2.16 \pm 0.721**	1.44	1.92
		SE	11.74 \pm 3.24			
	III	NW	38.68 \pm 5.76	2.48 \pm 4.100	8.61	11.80
		SE	36.20 \pm 11.62			
Ratio: Area of Xylem Area of Xylem Rays	I	NW	37.41 \pm 11.90	1.03 \pm 4.445	9.24	12.79
		SE	36.38 \pm 7.49			
	II	NW	37.14 \pm 3.60	2.03 \pm 3.102	6.52	8.93
		SE	39.17 \pm 9.12			
	III	NW	37.74 \pm 4.92	0.49 \pm 1.917	3.83	5.10
		SE	37.25 \pm 9.33			
Ratio: Area of Xylem Area of Xylem Rays	I	NW	5.03 \pm 0.70	0.10 \pm 0.407	0.86	1.17
		SE	5.13 \pm 1.08			
	II	NW	6.04 \pm 0.71	0.20 \pm 0.364	0.76	1.05
		SE	5.84 \pm 0.91			
	III	NW	6.58 \pm 0.68	1.22 \pm 0.280**	0.59	0.81
		SE	5.36 \pm 0.56			
	All	NW	5.89 \pm 0.94	0.45 \pm 0.211*	0.42	0.56
		SE	5.44 \pm 0.90			

Differences in all other anatomical features were not statistically significant.

Although Hanson (1917) did not consider leaves from the two sides of a tree, his results are similar to those obtained by the writer in that he observed

TABLE 2. (Continued)

Ratio: Area of Stele Area of Xylem Rays	I	NW	47.01 ± 19.63	5.31 ± 9.064	19.04	26.09
		SE	52.32 ± 20.89			
	II	NW	64.88 ± 12.24	1.20 ± 6.618	13.90	19.05
		SE	66.08 ± 16.98			
All	III	NW	75.40 ± 10.00	19.82 ± 5.434**	11.42	15.64
		SE	55.58 ± 13.98			
	III	NW	62.43 ± 18.42	4.44 ± 4.691	9.38	12.48
		SE	57.99 ± 17.92			
Ratio: Area of Non-stelar Tissues Area of Stele	I	NW	2.86 ± 0.28	0.29 ± 0.099**	0.21	0.28
		SE	2.57 ± 0.15			
	II	NW	2.49 ± 0.19	0.27 ± 0.080**	0.17	0.23
		SE	2.22 ± 0.16			
All	III	NW	2.25 ± 0.21	0.54 ± 0.081**	0.17	0.23
		SE	2.79 ± 0.15			
	III	NW	2.53 ± 0.34	0.00 ± 0.080	0.17	0.23
		SE	2.53 ± 0.28			
Number of Stomata	I	NW	185.0 ± 13.84	51.8 ± 12.434**	26.12	35.78
		SE	234.8 ± 36.80			
	II	NW	253.6 ± 9.42	65.5 ± 6.158**	12.93	17.72
		SE	189.1 ± 17.04			
All	III	NW	221.5 ± 14.85	45.5 ± 10.488**	22.04	30.18
		SE	267.0 ± 29.66			
	III	NW	219.4 ± 30.93	10.4 ± 9.930	19.86	26.41
		SE	229.8 ± 44.02			
Amount of Xylem in 0.00001 mm. ² per Stoma	I	NW	14.36	4.72		
		SE	9.64			
	II	NW	7.26	14.50		
		SE	21.76			
All	III	NW	14.62	1.83		
		SE	12.79			
	III	NW	11.71	3.45		
		SE	15.16			
Number of Resin Canals	I	NW	5.6 ± 1.43	3.4 ± 0.471**	1.0	1.4
		SE	2.2 ± 0.42			
	II	NW	2.1 ± 0.10	3.9 ± 0.504**	1.1	1.4
		SE	6.0 ± 0.16			
All	III	NW	5.3 ± 0.82	1.2 ± 0.495*	1.0	1.4
		SE	4.1 ± 1.20			
	III	NW	4.3 ± 1.86	0.2 ± 0.492	1.0	1.3
		SE	4.1 ± 1.94			
Number of Rows of Stomata	I	NW	18.1 ± 1.29	7.9 ± 1.048**	2.2	3.0
		SE	26.0 ± 3.06			
	II	NW	26.5 ± 1.51	7.2 ± 0.735**	1.5	2.1
		SE	19.3 ± 1.77			
All	III	NW	22.3 ± 1.06	6.5 ± 0.893**	1.9	2.6
		SE	28.8 ± 2.62			
	III	NW	22.3 ± 3.71	2.4 ± 1.232	2.5	3.3
		SE	24.7 ± 4.74			

a thicker cuticle on leaves from the south periphery of certain trees than on leaves from the center of the crown.

The difference in the thickness of the epidermis of needles from the southeast side as compared to the northwest side, although nonsignificant in the present study, is not in agreement with the results of Hanson (1917) and Büsgen and Münch (1929, p. 217) who found a thicker epidermis on leaves from the south periphery of a tree than on leaves from the center of the crown. Shank (1938) likewise noticed little difference in epidermal thickness of leaves from the north and south sides of certain trees during humid years but found a marked difference in dry years.

Considering the three trees as a group, the writer's results are similar to those obtained by Hanson (1917) who noted that leaves growing in the sun at the south periphery of certain trees were thicker than leaves growing in the shade at the centers of the trees. Shank (1938) observed thicker leaves from the south side of a tree as compared to the north side only during less humid years in the same study mentioned above.

Effects of exposure to wind.—As compared to trees on the lee slope, those individuals growing on the ridgetop which are so exposed to strong winds that the trees are deformed were found to have a significantly thicker cuticle, thinner epidermis, thicker hypodermis, shallower stomatal chambers, smaller cross-section area of needles, larger proportion of cross-section area of xylem to cross-section area of needle, larger proportion of cross-section area of xylem rays to cross-section area of xylem, larger proportion of cross-section area of xylem rays to cross-section area of stelar tissues, and higher stomatal frequency (Table 3).

Table 3. Analysis of data on the effects of wind exposure on needle structure.

Attribute	Series	Means with Standard Deviations	Diff. between Means with Std. Errors	Least Significant Mean Difference	
				5%	1%
Depth of Outer Stomatal Chamber	Exposed	23.01 \pm 2.74	1.22 \pm 0.274**	0.54	0.71
	Protected	24.29 \pm 2.01			
Thickness of Cuticle	Exposed	2.70 \pm 0.24	0.66 \pm 0.042**	0.08	0.11
	Protected	2.04 \pm 0.32			
Thickness of Epidermis	Exposed	12.18 \pm 1.00	0.71 \pm 0.305*	0.61	0.91
	Protected	12.89 \pm 1.34			
Thickness of Hypodermis	Exposed	31.45 \pm 3.68	6.68 \pm 0.879**	1.76	2.24
	Protected	24.77 \pm 3.10			
Cross-section Area of Needles in 0.1 mm. ²	Exposed	10.35 \pm 1.75	1.39 \pm 0.668*	1.34	1.78
	Protected	11.74 \pm 3.24			
Ratio: Area of Needle Area of Xylem	Exposed	32.27 \pm 5.70	4.98 \pm 1.996*	3.99	5.31
	Protected	37.25 \pm 9.33			
Ratio: Area of Xylem Area Xylem Rays	Exposed	4.59 \pm 0.92	0.85 \pm 0.235**	0.47	0.62
	Protected	5.44 \pm 0.90			
Ratio: Area of Stela Area Xylem Rays	Exposed	41.08 \pm 11.23	16.91 \pm 3.861**	7.72	10.27
	Protected	57.99 \pm 17.92			
Ratio: stelar Tissues Area of Stela	Exposed	2.62 \pm 0.31	0.09 \pm 0.076	0.15	0.20
	Protected	2.53 \pm 0.28			
Number of Stomata	Exposed	254.2 \pm 32.26	24.4 \pm 9.976*	19.95	26.54
	Protected	229.8 \pm 44.02			
Amount of Xylem in 0.0001 mm. ² per Stoma	Exposed	13.06	2.10		
	Protected	15.16			
Number of Resin Canals	Exposed	5.0 \pm 2.07	0.9 \pm 0.518	1.04	1.28
	Protected	4.1 \pm 1.94			
Number of Rows of Stomata	Exposed	22.9 \pm 2.57	1.8 \pm 0.988	1.98	2.63
	Protected	24.7 \pm 4.74			

The amount of xylem per stoma was found to be less in the needles of trees exposed to wind. However the significance of the difference is not known, since these data could not be analyzed statistically.

No significant difference was observed in regards to the other characters studied: proportion of cross-section area of stelar tissues to cross-section area of non-stelar tissues, number of resin canals per needle, and number of rows of stomata per needle.

The direction of gradient in depth of the outer stomatal chamber as observed in the present study is the opposite of that found by Kearney (1900), who noted that stomata were relatively deeper on the leaves of trees fully exposed to wind.

On the plants studied by Kearney (1900), he found that leaves exposed to wind had a thicker cuticle than protected plants. The writer observed the same effect in ponderosa pine needles. Studying the effects of artificially induced air movement, Cain and Potzger (1940) found the cuticle to be thicker on leaves of *Gaylussacia* exposed to wind than on those protected, even though the soil in the former case was kept moist. On leaves of plants grown in dry soil they observed very little difference in thickness of the cuticle with differences in air movement. The thickness of the epidermis varied in the same manner. The writer's results agree insofar as the cuticle was thicker on needles exposed to the wind, but with the pine the epidermis was found to be thinner on the exposed needles.

Leaves from plants growing on moist soil and under conditions of artificially induced air movement were found by Cain and Potzger (1940) to have a greater number of stomata per unit area than leaves of plants growing in moist soil but in still air. Martin and Clements (1935) also found the frequency of stomata on leaves to increase with increasing wind velocity. The results of the present study are in accord with both of these investigations.

Effects of height of insertion.—The height of insertion apparently has less effect on needle structure than any of the other environmental modifications (Table 4). Only the thickness of the hypodermis, and stomatal and resin canal frequencies were found to be significantly greater on the upper needles of the trees as compared to the basal needles.

The same type of variability between trees mentioned in connection with table 2 is also apparent in the data presented in table 4. Although significance is apparent when all three trees are treated as a unit, there can be no ecologic significance here if the gradient between individual trees is opposite from that between means of the groups of trees. Such is the case in the following comparisons which showed the upper needles to have thinner cuticle, larger cross-section area of needles, and a greater number of rows of stomata per needle.

No significant difference with either method of calculation was noted in most cases in regards to the depth of the outer stomatal chamber, thickness of the epidermis, proportion of cross-section area of xylem to cross-section area of needle, proportion of cross-section area of xylem rays to cross-section area of xylem, proportion of cross-section area of xylem rays to the cross-section area of stelar tissues, and the proportion of cross-section area of stelar tissues to cross-section area of non-stelar tissues.

The significance of the greater amount of xylem per stoma in the basal leaves as compared to the upper leaves could not be determined.

The results of the present study are not in agreement with the findings of

TABLE 4. Analysis of data on the effects of height of insertion on needle structure.

Attribute	Tree No.	Series	Means with Standard Deviations	Diff. between Means with St'd. Errors	Least Significant Mean Difference	
					5%	1%
Depth of Outer Stomatal Chamber	I	Tip	26.23 \pm 1.62	2.62 \pm 0.394**	0.79 ₄	1.05 ₄
		Base	23.61 \pm 1.42			
	II	Tip	25.20 \pm 1.46	0.53 \pm 0.446	0.89	1.19
		Base	25.73 \pm 1.96			
	III	Tip	21.73 \pm 1.73	1.82 \pm 0.344**	0.60	0.80
		Base	23.55 \pm 1.82			
Thickness of Cuticle	I	Tip	2.06 \pm 0.29	0.10 \pm 0.074	0.15	0.20
		Base	1.96 \pm 0.28			
	II	Tip	1.92 \pm 0.18	0.11 \pm 0.062	0.12	0.16
		Base	2.03 \pm 0.29			
	III	Tip	1.73 \pm 0.28	0.39 \pm 0.088**	0.18	0.23
		Base	2.12 \pm 0.40			
Thickness of Epidermis	I	Tip	14.33 \pm 1.22	2.74 \pm 0.399**	0.84	1.15
		Base	11.59 \pm 0.64			
	II	Tip	12.24 \pm 0.57	2.14 \pm 0.274**	0.58	0.79
		Base	14.38 \pm 0.65			
	III	Tip	12.68 \pm 0.69	0.02 \pm 0.334	0.70	0.96
		Base	12.70 \pm 0.80			
Thickness of Hypodermis	I	Tip	13.09 \pm 1.07	0.20 \pm 0.329	0.66	0.88
		Base	12.89 \pm 1.34			
	II	Tip	27.34 \pm 3.03	2.40 \pm 1.326	2.79	3.82
		Base	24.94 \pm 2.90			
	III	Tip	26.18 \pm 2.91	3.24 \pm 1.317*	2.77	3.79
		Base	24.94 \pm 2.97			
Cross-section Area of Needles in 0.1 mm. ²	I	Tip	26.75 \pm 2.92	2.31 \pm 1.489	3.13	4.28
		Base	24.44 \pm 2.70			
	II	Tip	27.42 \pm 2.91	2.65 \pm 0.777**	1.55	2.07
		Base	24.77 \pm 3.10			
	III	Tip	15.86 \pm 1.12	8.16 \pm 0.228**	0.48	0.66
		Base	7.70 \pm 0.90			
Ratio: Area of Needle Area of Xylem	I	Tip	10.14 \pm 0.55	4.45 \pm 0.509**	1.07	1.46
		Base	14.59 \pm 1.51			
	II	Tip	15.05 \pm 0.66	2.12 \pm 0.478**	1.00	1.38
		Base	12.93 \pm 1.36			
	III	Tip	13.68 \pm 2.69	1.94 \pm 0.769*	1.54	2.04
		Base	11.74 \pm 3.24			
Ratio: Area of Xylem Area of Xylem Rays	I	Tip	33.17 \pm 2.43	3.03 \pm 3.754	7.89	10.80
		Base	36.20 \pm 11.62			
	II	Tip	30.27 \pm 4.14	6.01 \pm 2.706*	5.68	7.79
		Base	36.38 \pm 7.49			
	III	Tip	39.89 \pm 4.96	0.72 \pm 3.266	6.86	9.40
		Base	39.17 \pm 9.12			
Ratio: Area of Xylem Area of Xylem Rays	I	Tip	34.48 \pm 5.59	2.77 \pm 1.985	3.97	5.28
		Base	37.25 \pm 9.33			
	II	Tip	6.13 \pm 0.72	1.00 \pm 0.412*	0.87	1.19
		Base	5.13 \pm 1.08			
	III	Tip	6.30 \pm 0.91	0.46 \pm 0.406	0.85	1.17
		Base	5.84 \pm 0.91			
Ratio: Area of Xylem Area of Xylem Rays	I	Tip	4.90 \pm 0.72	0.46 \pm 0.288	0.60	0.83
		Base	5.36 \pm 0.56			
	III	Tip	5.77 \pm 0.99	0.33 \pm 0.244	0.49	0.65
	All	Base	5.44 \pm 0.90			

Zalenski (1902), Yapp (1912), Heuser (1915), Stober (1917), Rippel (1919), and McDougall and Penfound (1928) who noted that the thickness of the cuticle increases with the height of the point of insertion of the leaf on the tree.

TABLE 4. (Continued)

Ratio: Area of Stele Area of Xylem Rays	I	Tip Base	61.64 ± 11.50 52.32 ± 20.89	9.32 ± 7.547	15.86	21.72
	II	Tip Base	59.61 ± 13.45 66.08 ± 16.98	6.47 ± 6.849	14.39	19.71
	III	Tip Base	54.49 ± 7.38 55.56 ± 13.98	1.09 ± 4.454	9.36	12.82
	All	Tip Base	58.56 ± 19.94 57.89 ± 17.92	0.59 ± 3.849	7.70	10.24
Ratio: Area of Non-stelar Tissue Area of Stele	I	Tip Base	2.56 ± 0.54 2.57 ± 0.15	0.01 ± 0.179	0.38	0.52
	II	Tip Base	2.28 ± 0.07 2.22 ± 0.16	0.01 ± 0.056	0.12	0.16
	III	Tip Base	2.56 ± 0.17 2.79 ± 0.15	0.23 ± 0.072**	0.15	0.21
	All	Tip Base	2.38 ± 0.35 2.53 ± 0.28	0.15 ± 0.082	0.16	0.22
Number of Stomata	I	Tip Base	247.0 ± 17.34 234.8 ± 36.80	12.2 ± 12.866	27.0	37.0
	II	Tip Base	295.2 ± 16.32 188.1 ± 17.04	107.1 ± 7.462**	15.7	21.5
	III	Tip Base	234.4 ± 27.51 267.0 ± 29.66	67.4 ± 12.791**	26.9	36.8
	All	Tip Base	292.2 ± 41.61 229.8 ± 44.02	62.4 ± 11.060**	22.1	29.4
Amount of Xylem in 0.00001 mm. ² per Stoma	I	Tip Base	19.39 9.64	9.75		
	II	Tip Base	11.47 21.76	10.29		
	III	Tip Base	11.40 12.79	1.39		
	All	Tip Base	13.66 15.16	1.50		
Number of Resin Canals	I	Tip Base	9.2 ± 1.55 2.2 ± 0.42	7.0 ± 0.508**	1.1	1.5
	II	Tip Base	7.9 ± 1.20 6.0 ± 0.16	1.9 ± 0.623**	1.3	1.8
	III	Tip Base	8.7 ± 0.82 4.1 ± 1.20	4.6 ± 0.459**	1.0	1.3
	All	Tip Base	8.6 ± 1.69 4.1 ± 1.94	4.5 ± 0.427**	0.8	1.1
Number of Rows of Stomata	I	Tip Base	24.2 ± 1.51 26.0 ± 3.06	1.8 ± 1.078	2.3	3.1
	II	Tip Base	32.0 ± 1.15 19.3 ± 1.77	12.7 ± 0.667**	1.4	1.9
	III	Tip Base	32.2 ± 2.15 28.8 ± 2.62	3.4 ± 3.386	7.1	9.7
	All	Tip Base	29.6 ± 3.98 24.7 ± 4.74	4.9 ± 1.129**	2.2	3.0

Zalenski (1902), Yapp (1912), Heuser (1915), and Stober (1917) all found an increase in thickness of the epidermis with increasing heights of insertion of leaves on trees, but such results were not consistently obtained with the three trees which the writer studied.

The results of the present study are in accord with those of Sorauer (1878), Zalenski (1902), Delf (1911), Yapp (1912), Heuser (1915), Rippel (1919), Rea (1921), Salisbury (1928), and Burt (1939) who found that with increasing height of the point of insertion of leaves on stems, the higher the stomatal frequency. Reed and Hirano (1931) found that the density of stomata was higher on the leaves near the ends of long shoots than on the basal leaves of the shoots, but the relationship was not well marked on short shoots.

Effects of age.—In contrast to young trees, old trees were found to have significantly thicker cuticle, thicker epidermis, thicker hypodermis, deeper outer stomatal chambers, larger cross-section area of needles, larger proportion of cross-section area of xylem to cross-section area of needle, larger proportion of cross-section area of xylem rays to cross-section area of stelar tissues, larger proportion of cross-section area of stelar tissues to cross-section area of non-stelar tissues, higher stomatal frequency per unit area, higher resin canal frequency per needle, and more rows of stomata per needle (Table 5).

More xylem per stomata was observed in needles of old trees than in young but the significance of the difference could not be determined.

TABLE 5. Analysis of data on the effects of age on needle structure.

Attribute	Series	Means with Standard Deviations	Diff. between Means with St'd. Errors	Least Significant Mean Difference	
				5%	1%
Depth of Outer Stomatal Chamber	Old	26.96 ± 2.44	3.47 ± 0.323**	0.64	0.84
	Young	23.39 ± 1.85			
Thickness of Cuticle	Old	1.99 ± 0.24	0.90 ± 0.028**	0.08	0.10
	Young	0.99 ± 0.27			
Thickness of Epidermis	Old	13.86 ± 1.76	3.35 ± 0.427**	0.85	1.14
	Young	10.51 ± 1.55			
Thickness of Hypodermis	Old	30.77 ± 3.24	9.15 ± 1.034**	2.07	2.75
	Young	21.62 ± 4.64			
Cross-section Area of Needles in 0.1 mm. ²	Old	16.82 ± 3.82	5.39 ± 0.954**	1.91	2.54
	Young	11.43 ± 3.56			
Ratio: Area of Needle Area of Xylem	Old	32.47 ± 4.99	10.65 ± 1.947**	3.89	5.18
	Young	43.12 ± 9.43			
Ratio: Area of Xylem Area Xylem Rays	Old	4.45 ± 0.64	0.61 ± 0.178**	0.36	0.48
	Young	5.06 ± 0.74			
Ratio: Area of Stele Area Xylem Rays	Old	45.25 ± 9.74	8.87 ± 3.377*	6.75	8.98
	Young	54.12 ± 4.97			
Ratio: Area of Non-stelar Tissues Area of Stele	Old	2.18 ± 0.40	0.88 ± 0.117**	0.23	0.31
	Young	3.06 ± 0.50			
Number of Stomata	Old	309.6 ± 32.51	93.8 ± 8.604**	17.2	22.9
	Young	215.8 ± 34.12			
Amount of Xylem in 0.00001 mm. ² per Stoma	Old	16.79	3.78		
	Young	13.01			
Number of Resin Canals	Old	9.8 ± 1.37	7.6 ± 0.259**	0.5	0.7
	Young	2.2 ± 0.38			
Number of Rows of Stomata	Old	32.8 ± 3.87	9.0 ± 1.020**	2.0	2.7
	Young	23.8 ± 4.03			

Discussion

The collections of needles in this study represent random samples in every case. By this method of sampling, a great deal of variation was encountered both between trees and among needles of individual trees, as is apparent in the tabular summaries of the data.

The data in tables 2 and 4 show that for many attributes the gradient of the difference between the means in one tree may be opposite to the gradient in another. A cursory examination of the data might suggest that such variations are due to errors in sampling technique. While this source of error may account for part of the variability, the statistical analyses indicate that the variation is primarily due to an inherent variability in the characters themselves.

A point of particular interest which this study has brought out is that one

tree may show a significant difference from the other two studied in one attribute, without exhibiting consistent eccentricity in other respects. For example, in regards to the depth of the outer stomatal chamber, tree III in table 2 shows a reversal from the gradient based on the group as a whole. However, the differences in the means of the thickness of cuticle on needles from trees I, II, and III are of the same order as the differences in the group means. Considering next the thickness of the epidermis, the reverse of the expected occurs not in tree III, as for the depth of the stomatal chamber, but in tree II. The eccentric individual with regards to the thickness of the hypodermis is tree III but in regards to the cross-section area of the needles it is tree I. Thus in these five attributes, results opposite from the differences in the group means have occurred at least once in all three trees comprising the group. The remainder of the data show the same variability.

In table 4 it is apparent that irregularities are of the same sporadic nature as those apparent in table 2. Likewise, it can be noted that for a particular attribute the reversal of gradients in individual trees as compared to the gradient of the differences between the groups is not always met in the same tree when different sets of environmental conditions are considered. This fact can be verified in another manner by comparing tables 2 and 4, since the data obtained for the southeast sides of the trees were used again for the bases of the trees in the tip-base comparisons.

The writer is unable to explain certain of these irregularities on the basis of the data accumulated thus far. In certain cases it is possible that an adequate sample was not obtained. However, in many of the collections there is reason to suppose that a good representation of the population has been obtained, in which case the anatomical variations must be considered of no ecologic significance.

Whereas in studying the effects of direction of exposure and height of insertion it is possible to analyze the data by individual trees, such is not the case when the effects of exposure to wind, effects of shade, and effects of age are considered. Here only the entire groups in each environment can be compared. Therefore, it is highly probable that were it possible to pair individual trees in contrasted environments, the same variability discussed for tables 2 and 4 would also be found to occur here.

In the light of the variability of certain anatomical characters, the necessity of using strictly comparable material in making comparisons of this kind cannot be over emphasized. Usually the limitations of small samples have been overlooked in the published researches on ecologic anatomy, and this may account for much of the disagreement in conclusions. Several important causes of variability must be recognized in studies on ecologic anatomy. There are hereditary influences, at the very least those due simply to heterozygosity, and errors of sampling, in addition to the environmental variations which are the primary objects of study. Since the biometric method aims to reduce certain of these errors and to reveal the presence of others, the advantages of its use in ecologic anatomy are evident.

Summary

Certain anatomical features of ponderosa pine needles taken from different natural environments were compared biometrically.

The effects of sun as contrasted to shade apparently produce the following statistically significant changes in the anatomical features of the needles: greater depth of outer stomatal chambers, thicker cuticle, thicker epidermis, larger cross-section area of needles, greater proportion of xylem in the needle, larger stele in proportion to non-vascular tissue, greater number of stomata per unit area, greater number of resin canals per needle, and greater number of rows of stomata per needle.

In comparing the northwest side of a tree with the southeast, only differences in the thickness of the cuticle were found to be significant. This structure proved to be thicker on the needles from the southeast sides.

As compared to trees on the protected lee slope, the needles of those exposed to strong winds were found to have a significantly shallower outer stomatal chamber, thicker cuticle, thinner epidermis, thicker hypodermis, smaller cross-section area of needles, larger proportion of cross-section area of xylem to cross-section area of needle, larger proportion of cross-section area of xylem rays to cross-section area of xylem, larger proportion of cross-section area of xylem rays to cross-section area of stelar tissues, and higher stomatal frequency.

In needles taken from the tips of trees, as compared to those from the base, the following significant differences in structure were observed: greater thickness of hypodermis, higher stomatal frequency, and greater numbers of resin canals.

The needles of old trees, in contrast to young trees, were found to have significantly deeper outer stomatal chambers, thicker cuticle, thicker epidermis, thicker hypodermis, larger cross-section area of needles, larger proportion of cross-section area of xylem to cross-section area of needle, larger proportion of cross-section area of xylem rays to cross-section area of xylem, larger proportion of cross-section area of xylem rays to cross-section area of stelar tissues, larger proportion of cross-section area of stelar tissues to cross-section area of non-stelar tissues, higher stomatal frequency per unit area, greater number of resin canals per needle, and greater number of rows of stomata per needle.

Certain of the conclusions reached in this study are not in accord with those of previous writers. Possibly this may be attributed to the fact that the biometric approach to ecologic anatomy has not been utilized to the extent that is necessary in view of the high degree of variability in plant structure.

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The Vegetation of the Edmund Niles Huyck Preserve, New York

Eugene P. Odum

Introduction

The Edmund Niles Huyck Preserve, which comprises about 500 acres adjoining the village of Rensselaerville, N. Y., is located about twenty-seven miles southwest of Albany on the Helderberg peneplain at an elevation of 1400 to 1700 feet. The Preserve was established and formally incorporated in 1931 by Mrs. Edmund Niles Huyck as a memorial to her late husband and in recognition of a need for the preservation of natural areas for recreation, education, and study. In addition to the protection of the native plants, animals, and the scenic beauty of the area, the construction of suitable trails, and the operation of a restricted camp ground, the officers of the Preserve felt that something more constructive should be done with the area so that it might become more than just another small sanctuary. At the suggestion of several prominent biologists, a Scientific Advisory Committee consisting of William J. Hamilton, Chairman, the late G. Kingsley Noble, Thomas Ordway, Lewis Eldridge, John R. Greeley, and William Vogt was appointed to consider the possibility of establishing a research biological station. During the summers of 1936 and 1937 Dr. Hamilton made a preliminary biological survey of the area and in 1939 a biological station was established with provisions for a Resident Biologist and several Summer Fellows to devote their full time to problems in field biology.

The writer had the good fortune to serve as the first Resident Biologist on the Preserve in 1939-40 and to return to the area as a Summer Fellow in 1941. Although primarily trained as a zoologist and animal ecologist, the writer undertook for several reasons to make a comprehensive vegetation survey of the area. First, a record of present conditions is highly desirable for evaluation of future changes and developments. For example, present day ecologists are often greatly handicapped by lack of records of past conditions. A second and more immediate reason was that a workable habitat classification was desired for use in intensive life history studies of birds. It was also hoped that such a survey would be useful to subsequent workers in the area. In a word, this paper might be considered a preliminary inventory of the natural "laboratory."

Methods

The Preserve was first divided roughly into general vegetation or community types as determined by observational appraisal. Frequent reconnaissance trips were made and the various communities plotted on mimeographed sec-

tional maps. A large map compiled from recent surveys was used as a basis for the vegetation map, and a series of airplane photographs of the area proved to be of much help. Secondly, these types were subdivided into areas which possessed ecological unity, that is, natural and artificial boundaries. Such areas were then numbered (Fig. 1) not only for purpose of the vegetation study but also to facilitate the location of observations of all kinds. Finally, some of the larger and more important plant communities were selected for more detailed study. Quantitative data were obtained by a simple strip or transect census method. A 500 foot string was laid down along a compass line. While proceeding along this string with a ten foot stick (hinged in middle), the trees, seedlings, and shrubs encountered five feet on either side of the

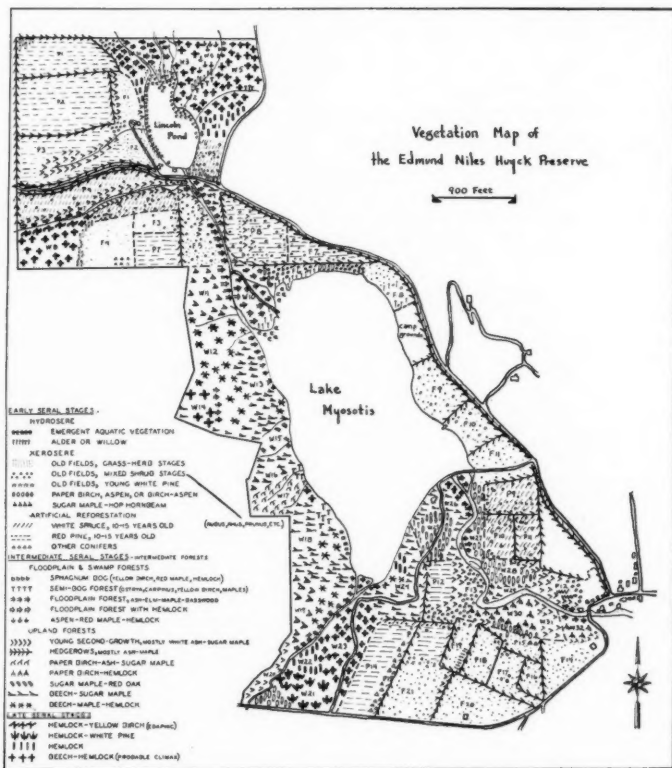


Fig. 1. Map of the Edmund Niles Huyck Preserve showing the principal plant communities.

string were classified and recorded. Each transect thus equalled 5000 sq. ft. or about $1/9$ acre. Tree species were listed under approximately the same four size classes as used by Lutz (1930) and others, namely: under 1 inch, 1-4, 4-10, and over 10 inches d.b.h. (diameter breast high). Shrubs were also enumerated. Small seedlings under two feet in height were not listed but included with the herb stratum. Herbs were not counted individually, but the principal species were noted and the percentage of ground covered by their foliage was estimated by means of a series of square yard quadrats laid out separately in the area. Collections were made of all dominants and sub-dominants listed and the identifications checked with Dr. Homer House, State Botanist. Nomenclature follows Gray's Manual, 7th edition, except in a few cases where authorities are given.

Transects were made after careful reconnaissance of the area so as to determine the best way to lay the strip to get the most representative sample. Edges, openings due to cutting, or stream borders were avoided. From one to five transects were made in each area, depending on the size and uniformity of the vegetation, resulting in a sample of 3 to 6 per cent.

Cain (1930, 1934, 1936, 1938) and others have made numerous investigations of sampling methods for forest plant communities. Three sample methods are commonly used: (1) a single large quadrat, (2) a strip transect, and (3) a series of small quadrats scattered equidistant over the area. The statistical results vary, sometimes rather widely, according to the method used even though the size of the sample is the same. For an area as a whole, however, the strip method gives a better sample than the single quadrat and the scattered quadrat method seems to give the best sample of all, but, of course, requires the most labor. Cain (1936) concludes that choice of methods depends ultimately on what one desires to illustrate and the time one has to devote to the study. The simple transect "touch" method was selected for this study principally because it seemed to be the easiest and quickest method of studying a wide variety of communities. The purpose of the samples was not so much to uncover hidden characteristics or phytosociological relations within the community, but to obtain a concrete expression of the whole which could be put on paper, could be used in comparisons (present and future), and which would convey a picture of the community to one who had not examined it. This method has an especial advantage for the zoo-ecologist who desires to spend the major part of his time in intensive study of particular species or problems within the community, but who desires a more accurate expression of the vegetation than can be obtained from simple observation alone.

General Description of the Area

The general character of the vegetation of the Huyck Preserve is shown in Fig. 1. On the legend accompanying the map, the plant communities are listed according to the general successional trends believed to be occurring. About 104 acres* of the Preserve consists of aquatic habitats (Lincoln Pond

* Areas determined by planimeter measurements of the completed map.

9.8 and Myosotis Lake 94 acres). Terrestrial habitats comprise about 373 acres of which 153 acres may be classified as early seral stages (about half artificially planted), 140 acres represent intermediate forests, and 80 acres are classed as mature or late seral stages.

Ten Mile creek, a tributary of Catskill creek, flows through the middle of the area being dammed at two places to form the two bodies of water. Hills on either side slope towards this valley, with the elevation varying from 1700 ft. (Area W-8) to about 1400 ft. (at Village). Between areas W29 and W30 the stream cuts a deep ravine resulting in the spectacular Rensselaerville Falls. The tributary stream between areas W7 and 8 also runs through a steep ravine. It is interesting to note that the moist north-facing slope of this latter ravine bears a mature stand of hemlock and yellow birch, a forest type generally restricted to bogs in this region but commonly found along shores of Adirondack lakes further north. Except for these two ravines, topographic conditions are not so extreme as to produce marked edaphic conditions.

The geology of the region has been well described by Goldring (1935). The Preserve is located almost entirely on the Oneonta geological formation of the non-marine Hamilton beds. The beds consist of alternate layers of greenish and reddish sandstones and shales, the latter giving road cuts of the region a characteristic reddish color. At the extreme southeastern part of area, below the Falls, marine Hamilton beds occur. The soils of the area have not been studied; in many places the soil is relatively thin and rocky, and unsuited for agricultural purposes.

As can be readily seen from Fig. 1, a great variety of plant communities are present with no one type occupying extensive or contiguous areas. This results in numerous intermediate zones between types, fragments, and forest edges which can not be adequately classified, numbered or mapped. Nevertheless, these are very important to the area as a whole, since it is usually found that the more "edges" or variation in the habitat, the greater the number of plants and animals. From the standpoint of biological productivity, it may be desirable to maintain artificially some of this variation in the future, but this should be done only according to a definite plan and, above all, artificial changes should be recorded if future evaluation of natural changes is to be possible.

The general character of the vegetation of this region has been well described by Nichols (1935) in his discussion of the hemlock-white-pine northern hardwood region, which extends as a broad belt of territory from New England to northern Great Lakes region. The region is also known as pine-hemlock association (Weaver and Clements, 1938). Considered more broadly, the Preserve lies in the ecotone between the well-marked northern or trans-continental coniferous forest region or biome and the eastern deciduous forest region or biome (see Shelford and Olson, 1935; Pitelka, 1941). It is an excellent example of an ecotonal region where plants, animals, and climate show characteristics intermediate between two major regions. In this

connection a difference in viewpoint between the plant and animal ecologist is well illustrated. The plant ecologist tends to give the hemlock-white-pine-northern hardwood region the rank of a major formation, as did Nichols, because several important dominants are characteristic of and largely restricted to it, for example, — the white pine, eastern hemlock, and the yellow birch. On the other hand, the animal ecologist prefers to consider the region as an ecotone because there are few important animals that are restricted to it; the important animal life (particularly of the mature stages) is rather a mixture of species characteristic of both coniferous and deciduous regions.

The area is well buffered by surrounding territory of a similar nature. In common with large sections of hill country in the northeast, the region was formerly more agriculturally prosperous and more thickly populated than at the present time. With the opening of more fertile lands to the west, many farms have been abandoned during the past several decades. It has been estimated that the farm area in New York alone has been reduced nearly 5,000,000 acres between 1880 and 1930. As a result, much land is being reclaimed naturally or by the government and is being used for recreation, forestry, and wildlife purposes. Old stone walls and former foundations are frequently seen nearly obliterated by returning forests, while lilac bushes and apple trees are waging a losing battle against young native second growth. The gradual change from complete human domination with its destruction of native plant and animal life to a natural or semi-natural state is not only a dramatic and interesting process to study, but also one that has considerable significance concerning the future rôle of agriculturally sub-marginal lands.

A number of the abandoned fields on the Preserve (the P series on the map) were planted during the years 1927-30 with pure stands of conifers largely red pine (*Pinus resinosa*) and white spruce (*Picea canadensis* probably mixed with *P. abies*), which are not native to the region. Many of these plantations, especially the pine are doing well and some will doubtless mature into even-aged stands, but in the face of competition with native species it is unlikely that they will reproduce themselves (unless artificially propagated). What actually happens here, of course, is the establishment of an artificial early seral stage which, if there is no further interference, will eventually be replaced by the native climax, provided of course that native climax species are not exterminated. The type of reforestation, involving use of even-aged dense stands of conifers, has been practiced for many years in Europe and has been widely recommended in this country for quick production of marketable timber on idle lands so badly depleted that natural reforestation is slow in starting. From study of plantations on the Preserve, it is evident that planted areas have a greater basal area than unplanted ones at present (15-20 years after planting), and hence will probably produce usable timber more quickly. For example, area P7 now has a basal area of approximately 50 sq. ft. per acre (about 1000 pines per acre) as compared to the adjacent unplanted area F3 which has a basal area of less than 10 sq. ft. (about 250 trees, mostly cherry and birch, over 1 in d.b.h.).

However, from the long-time ecological standpoint there are a number of disadvantages to this type of reforestation. Use of non-endemic species in pure stands reduces such plantations to the category of a cultivated crop of trees which like all crops requires attention for maintenance, and which sometimes are especially subject to the spread of disease and parasites (the white spruce of the area are already infested with the potentially dangerous spruce saw-fly, *Gilpinia polytoma*). Even-aged stands of conifers are generally less interesting to the nature lover, and, as far as limited studies show, are inferior to natural forests in abundance and variety of wildlife (see Leopold, 1936). Finally, such stands do not lend themselves well to the more modern forestry practices of selective cutting and continuous yield production. The presence of these plantations growing along side of natural reforestations on the Preserve provides a good opportunity for further work on the problem of artificial vs. natural reforestation, particularly as it effects the animal population.

Quantitative Data

Quantitative data for eleven of the more characteristic and interesting forested areas are summarized in Tables 1-5. The density of tree species by the four size classes previously mentioned, the basal areas (BA), the percentage of total basal area (%), and the general character of shrub and herb layer are given in these tables. All figures are on an acre basis. Basal area figures are only approximate since they were computed from average basal areas of three larger size classes plus values for large trees over 20 inches d.b.h. which were measured individually (thus, figures represent all trees over 1 inch d.b.h.). The basal area values, therefore, are useful for intercomparisons but probably should not be compared with results of studies where areas of all trees were computed individually. With exception of area W10 which is on a floodplain and area W30 which is on a north facing ravine slope, all these communities are on level or moderately sloping upland.

The principal species of herbs of the various plant communities are as follows:

Areas W1, 2, 3, 5, 8, 21, 30 (Tables 1 & 2). *Dryopteris spinulosa* var. *intermedium* (Muhl.), *Lycopodium complanatum* (area W30), *Mitchella repens*, *Clintonia borealis*, *Oxalis acetosella*, *Trientalis borealis*, *Maianthemum canadense*, *Waldsteinia fragarioides*, *Tiarella cordifolia*, *Veronica officinalis*, *Galium triflorum*, *Pyrola secunda*, *Viola rotundifolia*.

Areas W12, 18 (Table 3). Numerous species, the most important of which are: *Caulophyllum thalictroides*, *Aster macrophyllus*, *Aster divaricatus*, *Athyrium asplenoides*, *Dryopteris marginalis*, *Dryopteris spinulosa*, *Viola rotundifolia*, *Aralia nudicaulis*, *Waldsteinia fragarioides*, *Adiantum pedatum*, *Polystichum acrostichoides*, *Medeola virginiana*, *Mitchella repens*, *Mitella diphylla*, *Botrychium virginianum*, *Veronica officinalis*, *Arisaema triphyllum*, *Smilacina racemosa*, *Actaea rubra*, *Gaultheria procumbens*, *Hepatica* sp., *Trillium* sp.

Area W10 (Table 4). *Eupatorium utricaeifolium*, *Solidago flexicaulis*, *Impatiens biflora*, *Psedera quinquefolia*, *Thalictrum polygamum*, *Prenanthes altissima*, *Nepeta hederacea* (vine), *Clematis virginiana* (vine), *Geum virginianum*, *Circaea lutetiana*, *Sium ciculaefolium*. In forest openings: *Eupatorium perfoliatum*, *E. purpurcum*.

Area W11 (Table 4). First six species in W10 and: *Adiantum pedatum*, *Polystichum acrostichoides*, *Athyrium asplenoides*.

Area W17, W25 (Table V) *Eupatorium urticaefolium*, *Solidago flexicaulis*, *Caulophyllum thalictroides*, *Aster macrophyllus*, *Solidago graminifolia*, *Potentilla canadensis*, *Smilacina racemosa*, *Pteris aquilina* (Area W25), and numerous others.

Supplementary notes: Area W8.—Large hemlocks and beeches removed from one corner of the area resulting in pitches of second growth maple, ash, basswood. Stripped maple, ordinarily a small understory tree grows to large size in these openings. Area W10.—Several old dead apple trees indicate this area was once cleared. Area W11.—Numerous dead stubs of *Prunus pennsylvanica* indicate area was once entirely cleared. Area W17. A low moist area; hemlock are seeding in clumps in the characteristic manner. Area W18. Numerous large hemlock stumps in this area indicating comparatively recent removal without complete clearing of land.

A comparison of several dynamic aspects of these plant communities is shown in Figs. 2 and 3. Despite differences in site, relative age, and previous land use history, several important trends are brought out when areas are arranged in the approximate order of succession (see later discussion). Thus, basal area is closely related to density of larger trees (over 10 in. d.b.h.), especially in older forests, and both increase as the forest matures (Fig. 2).

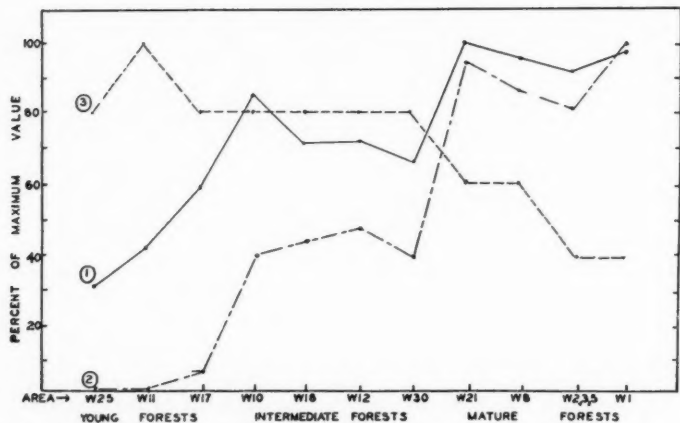


Fig. 2. Comparison of successional dynamics of eleven areas. (1) Basal area. (2) Density of trees 10 inches d.b.h. and over. (3) Number of dominant species comprising 90 per cent of the basal area (maximum number is five).

The number of dominant species, on the other hand, decreases. Using percentage of basal area as a criterion of dominance, we find that in younger forests 90 per cent of the basal area is distributed among four or five dominants, while in more mature communities there are only two or three (virtually one in area W1) dominants according to the same criterion (curve 3, Fig. 2). In Figure 3 the total density figures for three forest layers are plotted on a percentage basis. The density of herbs is inversely correlated with density of large trees (superior arborescent layer), as is generally the case, whereas the shrub layer (including seedlings) tends to reach greatest density in the inter-

mediate forests. Herb development is poor under all hemlock stands (last 5 areas, Fig 3) regardless of basal area, probably to be correlated with high soil acidity (see Daubenmire, 1931). The shrub layers of these more mature communities are made up largely of the seedlings of the dominants (except for locally prominent *Taxus canadensis*).

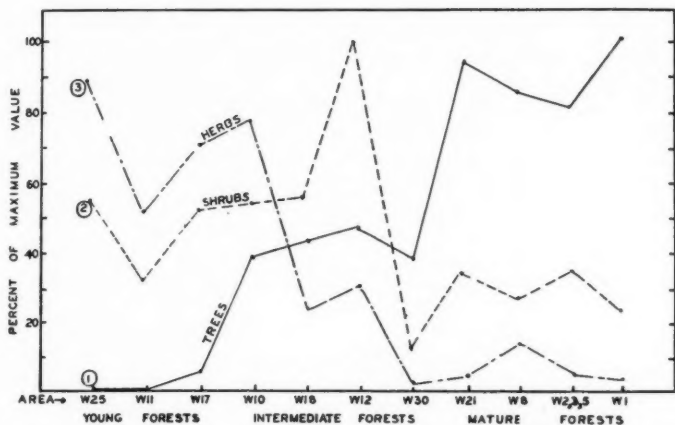


Fig. 3. Comparison of successional dynamics of eleven areas. (1) Density of trees 10 inches d.b.h. and over. (2) Density of shrubs and seedlings (under 1 inch d.b.h.). (3) Herb density in average percent of ground covered by foliage.

Climax

There is no virgin forest on the Preserve nor in the general area; a few scattered large trees may represent a remnant of primeval timber. All early accounts indicate that eastern hemlock was prominent in the original vegetation. The density of large stumps in some areas near Rensselaerville indicates that small areas at least were originally nearly pure stands of this species. Practically all the virgin hemlock was cut off by latter part of the 19th century when the bark was in great demand for tanning. Tanneries located in Rensselaerville were discontinued in the 1870's as nearly as can be learned from old residents. Parts of the Preserve have been owned by the Huyck family since 1900 and have not been greatly disturbed for some time (some beech and a few dying hemlocks have been removed for firewood from time to time, especially in Area 5). Consequently, small areas of fairly mature forests have developed. Judging from the composition of these oldest areas (Table 1), together with the above evidence, it appears that the climax of the region is the beech-hemlock association, or the hemlock consociation, or both intermixed. As can be seen from Table 1, beech-hemlock is reproducing itself well with numerous seedlings and trees of all size classes, but with hemlock

predominating over beech about two to one (average of three areas). Other reproduction is, at present, comparatively unimportant. In other communities of the Preserve, on the other hand, the reproduction is generally different (in kind or proportion) from the dominants, forecasting a future change. The beech-hemlock type also occurs on a wide variety of places, including sites from a few feet above water (Area W2), on sloping topography (area W5 and W23), and high on level upland (area W8 or W14).

This climax is similar to the virgin Hearts Content forest (Lutz, 1930); (Morey, 1936), the East Tionesta forest (Hough, 1936) of western Pennsylvania, and the Big Basin in Allegheny State Park, New York (Gordon, 1940). The East Tionesta area is especially interesting since Hough (1936) considers it the largest single tract of virgin forest between the Adirondacks and the Smokies, and he believes that the plant community is more mature than in adjacent virgin forests (Hearts Content and Cook forest). The proportion of dominants in this forest by basal area is hemlock, 63 per cent; beech, 20 per cent; sugar maple, 4 per cent; yellow birch, black birch, and red maple 3 per cent each, which is similar to beech-hemlock forests on the Preserve (see Table 1). The shrubbery and herbaceous vegetation is also strikingly similar since the principal species in the Tionesta area as well as the Big Basin (Gordon, 1940, p. 35) consist of *Viburnum alnifolium*, *V. acerifolium*, *Dryopteris spinulosa*, *Oxalis acetosella*, *Mitchella repens*, *Maianthemum canadense*, *Tiarella cordifolia*, *Lycopodium lucidulum* (compare Table 1 and Herb list above). However, the beech-hemlock on the Preserve is much younger than that of the above mentioned areas since trees over 25 inch d.b.h. are rare. A number of hemlock stumps can be found in the region which measure 30-40 inches or more across showing that the original hemlocks were nearly as large as virgin ones in Pennsylvania. Area W3 is the least disturbed beech-hemlock on the Preserve, but is very small. Area W8 has largest individual trees but is not uniform due to previous cutting. Beech, sugar maple, and stripped maple have formed dense growths in several places where removal of large trees released them from suppression.

Daubenmire (1931) and Oosting and Billings (1939) have shown that the soil under hemlock stands is extremely acid (pH 3 to 4.7) which seemingly tends to prevent invasion of deciduous species. On the Huyck Preserve, beech, among deciduous dominants, seems best able to reproduce under hemlock as shown by the large number of small trees and seedlings in Areas W1, 2, 3, 5, 8 (Table 1). Yellow birch, although less frequent, seems to be able to grow and reproduce with hemlock especially in moist situations. Sugar maple, on the other hand, a prolific species and abundant in second growth (Table 4, 5), does not occur to any great extent with heavy stands of hemlock. If the data on Tables 1 and 3 are compared it will be seen that as hemlock increases in basal area the sugar maple decreases to a much greater extent than does beech. This difference in the two species is interesting in view of the fact that they are usually considered to have nearly identical ecological requirements (Weaver and Clements, 1938, p. 510). Where the soil is thin or other conditions especially favor hemlock it is probable that a

nearly pure stand of hemlock is the ultimate development, beech being the last deciduous species to be excluded. Even in the hemlock consociation of Area W1, however, a large number of beech seedlings are present, many obviously heavily suppressed but ready to take advantage of the first opening in the hemlock crown.

The probable rôle of the white pine in climax of the eastern hemlock region is fully discussed by Nichols (1936). Observations in the Helderberg region support his contention that the white pine occurred as a normal, although minor, constituent of the primitive climax forest; and dense stands are distinctly sub-climax resulting from fire or other disturbance. On the Preserve, white pine is prominent only in area W21 where large individuals are mixed with hemlock. As can be seen from Table 2, white pine is not reproducing as well as either hemlock or beech, and most of the seedlings are in artificial openings. Because of the great age achieved by the white pine, however, pine or pine-hemlock stages may persist for very long periods and apparently may attain a greater basal area than the climax.

Successional Relationships

Conditions for studying the dynamics of succession or the development of the climax are very favorable in the region because of the large number of different stages within a relatively small area. Details of succession are a study in themselves and beyond the scope of this paper, but a brief account is necessary in order to indicate the relation and the relative stability of the various plant communities mapped in Fig. 1. Fig. 4 is a simplified diagram

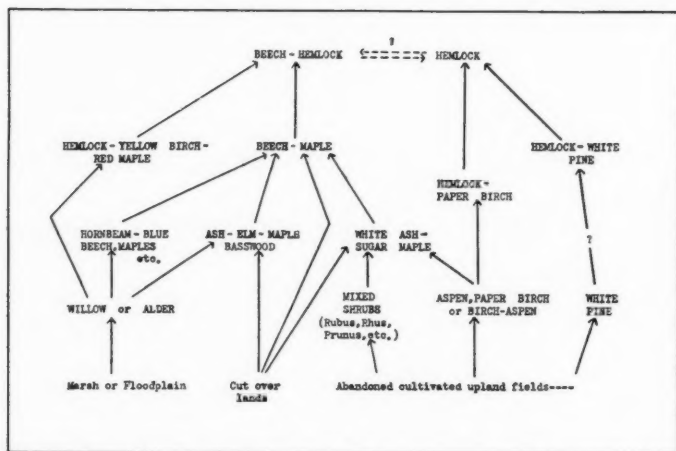


Fig. 4. Simplified diagram of successional relations on Edmund Niles Huyck Preserve. See text for details.

TABLE 2

Trees:	AREA W21 (4.6 Acres)						AREA W30 (3.3 Acres)					
	Hemlock-White Pine Associates						Hemlock-Paper Birch Associates					
	Size Classes				BA	%	Size Classes				BA	%
	1	2	3	4			1	2	3	4		
<i>Tsuga canadensis</i> (L.) Carr.	52	20	45	45	76	36	78	96	43	26	54	39
<i>Pinus Strobus</i> L.	20	7	20	72	105	50
<i>Betula papyrifera</i> (Marsh.)	7	20	7	3	1	12	78	12	41	30
<i>Fagus grandifolia</i> Ehrh.	26	7	26	8	4	20	39	12	9
<i>Acer saccharum</i> Marsh.	20	7	7	10	5	26	12	12	21	15
<i>Betula lutea</i> Michx.	12	4	3
<i>Prunus serotina</i> Ehrh.	33	12	12	12	4	3
<i>Acer rubrum</i> L.	39	39	12	6	3
<i>Fraxinus americana</i> L.	7	6	2	1
<i>Quercus borealis</i> Michx.	7
<i>Ostrya virginiana</i> (Mill.) Koch	7
<i>Acer pennsylvanica</i> L.	33	33	7	4	1	12
Totals	244	152	117	124	212	100	98	158	205	50	138	100
Shrubs:												
<i>Acer spicatum</i> Lam.	104										
<i>Taxus canadensis</i> Marsh.	a few patches						Dense patches (numerous)					
Others	13										
Herbs: (See Text)												
Total Coverage	6%						1%					

TABLE 3

Trees:	AREA W12 (13 Acres)						AREA W18 (7.4 Acres)					
	Beech-maple-hemlock Associates						Beech-maple Associates					
	Size Classes				BA	%	Size Classes				BA	%
	1	2	3	4			1	2	3	4		
<i>Tsuga canadensis</i> (L.) Carr.	100	44	4	16	25	16	20
<i>Fagus grandifolia</i> Ehrh.	139	126	44	44	80	52	58	85	39	20	43	28
<i>Acer saccharum</i> Marsh.	631	309	22	4	27	18	314	143	92	26	71	47
<i>Betula lutea</i> Michx.	4	13	4	3	7	7	13	20	13
<i>Tilia americana</i> L.	30	52	17	8	5	54	46	2	2
<i>Fraxinus americana</i> L.	44	26	9	4	3	78	26	7	3	2
<i>Ostrya virginiana</i> (Mill.) Koch	9	44	2	1	39	72	13	7	5
<i>Carpinus caroliniana</i> Walt.	17
<i>Acer pennsylvanica</i> L.	56	65	3	2	13	72	7	5	3
Totals	1009	622	109	64	153	100	576	451	158	59	151	100
Shrubs:												
<i>Viburnum alnifolium</i> Marsh.	48						22					
<i>Hamamelis virginiana</i> L.	11						4					
Others	5										
Herbs: (See Text)												
Total Coverage	32%						25%					

of the way in which natural reforestation occurs as indicated by general observations on the Preserve and surrounding area. Succession (or in reality invasion) begins from three principal substrates as indicated: (1) relatively restricted marsh and floodplain areas, (2) numerous abandoned cultivated or pastured fields, and (3) areas more or less cut over but not cultivated. Lincoln Pond (Fig. 1) has a broad zone of emergent aquatic vegetation around most of its shore. *Glyceria grandis*, *G. borealis*, *Sagittaria latifolia*, var. *gracilis*, *Zizania aquatica* (introduced), and *Equisetum fluviatile* (largely upper end of pond) are the principal dominants. *Typha latifolia* occurs at present in only a few patches. Except in the deeper parts most of bottom of the pond is covered by a jungle of submerged plants (not indicated in Fig. 1) principally *Nitella* and *Chara*. Lake Myosotis has a generally sharp shore line or beach with little marsh vegetation except at the inlet where dominants are similar to the above, but with *Typha* more prominent.

Abandoned upland fields are commonly covered with numerous species of herbs and grasses for a number of years before woody plants invade. On the Preserve the principal dominants of this early stage are: (for example Areas F3 and 4) *Anaphalis margaritacea*, *Antennaria neodioica*, *Ranunculus acris*, *Danthonia spicata*, *Poa compressa*, *Fragaria vesca*, *Potentilla canadensis* (simplex), *Rumex acetosella*, *Hieracium aurantiacum*, *H. florentinum*, *Chrysanthemum leucanthemum*, var. *pinnatifidum*, *Solidago juncea*, *S. graminifolia*. These fields undergo considerable change in seasonal appearance. In early summer they are yellow and orange with a profusion of *Ranunculus* and *Hieracium* blooms; in mid-summer they are white with daisies; and in late summer become yellow again with goldenrods.

Natural reforestation seems to occur in four principal ways (or to follow 4 principal seres) as indicated in Fig. 4: (1) White pine often completely recaptures fields by seeding in as a dense stand. This tends to result in an even-aged, relatively uniform stand in which hemlocks and deciduous trees gradually become established. This type occurs only to a limited extent on the Preserve itself. One reason, at least, is the scarcity of old white pines which would provide seeds. (2) Paper birch (also *Betula populifolia* at lower altitudes), aspen (both *P. tremuloides* and *grandidentata*), or birch-aspen are common early seral stages, particularly on ravine slopes or along streams. Area W24 (Table 5) is an example of a mature birch-aspen stage. Hemlock often seed in at the base of birches resulting in old birch and young hemlock mixtures as an intermediate associates (Area W30, Table 2), or aspen-birch may be invaded by ash-maple or beech-maple stages (Area W17, Table 5). (3) On low ground alder (*Alnus incana*) and willow are prominent early invaders. These may be followed by deciduous floodplain forests (Area W10, Table 4) or a swamp or bog forest of red maple, hemlock, and yellow birch. (4) Blackberry (*Rubus*) sumac (*Rhus typhina*), thorn apple (*Crataegus*), pin and choke cherry (*Prunus pennsylvanica* and *P. virginiana*), shadbush (*Amelanchier*), ash (*Fraxinus americana*), and other quick growing shrubs and trees most frequently make up the early seral stages on the Preserve

TABLE 4

Trees:	AREA W10 (8.3 Acres) Ash-Elm-Maple-Basswood Associates						AREA W11 (6.0 Acres) Sugar Maple-Hop Hornbeam Associates					
	Size Classes						Size Classes					
	1	2	3	4	BA	%	1	2	3	4	BA	%
<i>Acer saccharum</i> Marsh.	109	70	56	9	33	18	170	464	65	42	46
<i>Fraxinus americana</i> L.	22	48	122	13	58	32	20	39	20	8	9
<i>Ulmus americana</i> L.	17	36	44	31	55	30	6	6
<i>Tilia americana</i> L.	39	39	48	5	24	13	33	26	13	5	6
<i>Ostrya virginiana</i> (Mill.) Koch.	9	6	261	6	14	15
<i>Tsuga canadensis</i> (L.) Carr.	4	39	58	20	9	10
<i>Juglans nigra</i> L.	4	4	4	7	4	6	2	2
<i>Carpinus caroliniana</i> Walt.	36	82	4	2	6	6
<i>Prunus serotina</i> Ehrh.	4	1	1	6	2	2
<i>Betula lutea</i> Michx.	13	6	3	4
<i>Quercus borealis</i> Michx.	13	4	4
<i>Populus tremuloides</i> Michx.	6
<i>P. grandidentata</i> Michx.	6	2	2
Totals	223	293	278	53	182	100	280	279	160	0	91	100
Shrubs:												
<i>Prunus virginiana</i> L.	360						72					
<i>Sambucus canadensis</i> L.												
<i>Rubus odoratus</i> L.												
<i>Hamamelis virginiana</i> L.												
Herbs: (See Text)												
Total Coverage	79%						50%					

(mixed shrub stage). Birds are supposed to play an important part in the establishment of these by dispersing the fruits. Also these species are prominent in the numerous hedgerows (See Fig. 1), facilitating invasion into adjoining fields. Such shrubby growths are followed by ash-sugar maple, maple, or beech-maple stages.

The above may occur, of course, in combinations resulting in seral stages having one or more types in competition. Aspen or birch may occur in combination with pin cherry and ash on abandoned fields. In area W4 a swamp forest of red maple and yellow birch is competing with hemlock and sugar maple to succeed an old large-toothed aspen stage (large individuals of latter still standing and many aspen logs). Extensive seepage areas on hillsides may favor a combination of bottomland and upland stages as in Area W11 (Table 4).

Succession may apparently take a short cut where land is cut over but not cultivated (see Fig. 4). Also, if the forest is only partially removed, a mixed community of old and new results, as is illustrated by a great deal of the woods along west shore of Myosotis lake (Areas W12, 13, 18) where scattered old hemlocks and beeches occur with young beech-maple. This beech-maple-hemlock type is widespread in sections of New York where virgin hemlock was removed by logging operations that did not entirely clear the land (for example, Alleghany State Park, Saunders, 1936).

TABLE 5

Trees:	AREA W17 (4.1 Acres)						AREA W25 (3.7 Acres)					
	Size Classes				Birch-Maple-Ash Associates		Size Classes				Birch-Aspen Associates	
	1	2	3	4	BA	%	1	2	3	4	BA	%
<i>Acer saccharum</i> Marsh.	314	417	26	...	27	21	10
<i>Fraxinus americana</i> L.	108	65	92	...	32	25	78	13	1	1.5
<i>Betula papyrifera</i> (Marsh.)	92	8	40	32	78	144	78	...	31	45
<i>Tilia americana</i> L.	65	26	13	...	5	4
<i>Ostrya virginiana</i> (Mill.) Koch	...	274	26	...	21	17
<i>Fagus grandifolia</i> Ehrh.	13	26	1	1
<i>Tsuga canadensis</i> (L.) Carr.	39	6
<i>Populus tremuloides</i> Michx.	183	261	26	...	20	29
<i>P. grandidentata</i> Michx.	4	26	26	...	9	13
<i>Prunus pennsylvanica</i> L.	52	144	7	10
<i>Acer rubrum</i> L.	39	13	1	1.5
Totals	539	808	249	8	126	100	450	601	130	0	69	100
Shrubs:												
<i>Viburnum acerifolium</i> L.	...	15	0
<i>Alnus incana</i> (L.) Moench.
<i>Rubus</i> , sp.	144
<i>Diervilla lonicera</i> Mill.
<i>Spiraea latifolia</i> Borkh.
Herbs: (See Text)												
Total Coverage	...	70%	90%

Summary

1. The Edmund Niles Huyck Preserve adjoining the village of Rensselaerville is a 500 acre tract located on the Helderberg peneplain of east-central New York at an elevation of 1400 to 1700 feet. It is incorporated and privately endowed as a natural area for recreation, education and study. A biological station was established in 1939 for purpose of promoting research in problems of field biology.

2. Twenty-six plant communities were recognized and mapped in the preliminary vegetation survey; these are arranged according to successional trends believed to be occurring. About 104 acres of Preserve consists of aquatic habitats, 153 acres may be classed as early seral stages (about half artificially reforested conifers), 140 acres as intermediate forests, and 80 acres as mature forests or late seral stages.

3. Quantitative data obtained by use of transects are tabulated for eleven of the more important areas. Density of trees by four size classes, basal area, percentage of basal area, and the general character of shrub and herb layers are given.

4. Several dynamic aspects of succession are plotted graphically. Basal area is closely correlated with density of large trees, both increasing as the forests mature. The number of dominants, on the other hand, decreases from 4 or 5

in young stages to 3, 2 or 1 in older ones. Density of trees and herbs is inversely correlated, whereas the shrub layer tends to reach maximum development in the intermediate forests.

5. Various evidence indicates that the climax of the region is the beech-hemlock association or the hemlock consociation or both intermixed. Small areas of relatively undisturbed but young climax forest are present on the Preserve.

6. Successional relations are diagrammed in order to relate the various communities and to indicate their relative stability. Natural succession on abandoned lands follows four principal seres as indicated by the following early seral stages (1) Willow or alder leading to a deciduous floodplain forest (ash-elm-maple-basswood) or swamp or bog forest (red maple, yellow birch, hemlock). (2) Paper birch, aspen, or birch-aspen followed by ash-maple or paper birch-hemlock. (3) White pine, probably developing into white pine-hemlock. (4) Mixed shrubs, *Rubus*, *Rhus*, *Prunus pennsylvanica*, *P. virginiana*, *Crataegus*, *Amelanchier*, etc., leading to ash-sugar maple and beech-maple.

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Variations in the Cabin Run Forest, a Climax Area in Southwestern Ohio

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Introduction

The Cabin Run area, an example of relatively undisturbed deciduous forest, is situated in middle eastern Clermont County, east of Cabin Run and one mile north of its junction with the East Fork of the Little Miami River. This forest, one-half mile long, lies near the southern limits of the Till Plains of the Central Lowland. The thick deposit of till entirely obscures the underlying Ordovician strata. The upland at an elevation of 860 feet has been maturely dissected by intermittent streams; the relief is 120 feet. The north and south ravines of the area connect with Cabin Run; smaller ravines end at the lateral limits of the stream terraces, dumping their load in gentle deltaic slopes; their water seeping through the loose gravel to the creek.

All the soil in this area is derived from glacial till. Since that is essentially uniform, the soil types are then the result of unequal leaching and of reaction to the occupying forests. Two soil types are here recognized, the Fairmount silty clay loam, and the Cincinnati silt loam (Taylor, A. E., et al., 1928). Their distribution is shown on the soil map (Fig. 1). In the ravines and on the valley slopes (the Fairmount silty clay loam area), leaching has removed calcareous fragments from the soil to a depth of one foot. The "A" horizon is neutral; the soil becomes basic within one foot of the surface. This soil type supports mixed deciduous forest. The intermittent streams erode this soil and deposit it at the base of the valley slopes, where soil horizons are obscured. Here, beech communities occur.

In the area occupied by the Cincinnati silt loam, drainage is good and percolation is rapid, resulting in greater leaching than in the former type. The "A" horizon, dark grey-brown, is underlain by soil gradually becoming dense, and changing to a calcareous plastic clay at 10 feet. The "A" horizon is generally acid and is overlain by mor (Heiberg, S. O., 1937). This type supports oak-hickory and beech communities.

In the century and a half of habitation of Clermont County most of the original forest has been removed. The Cabin Run forest is a remnant of this forest. Local fires have occurred. A fire in 1925 affected the southeastern part, burning only scattered trees. Red foxes, escaped from hunts, have locally disturbed the understory with trails, play areas and dens.

The vegetation of the Cabin Run forest varies in response to soil moisture, slope exposure and resulting microclimatic conditions. Seral communities are lacking (except for very local subseres). Conditions of reproduction and canopy features indicate that the vegetation has reached stability, yet is composed of many variations.

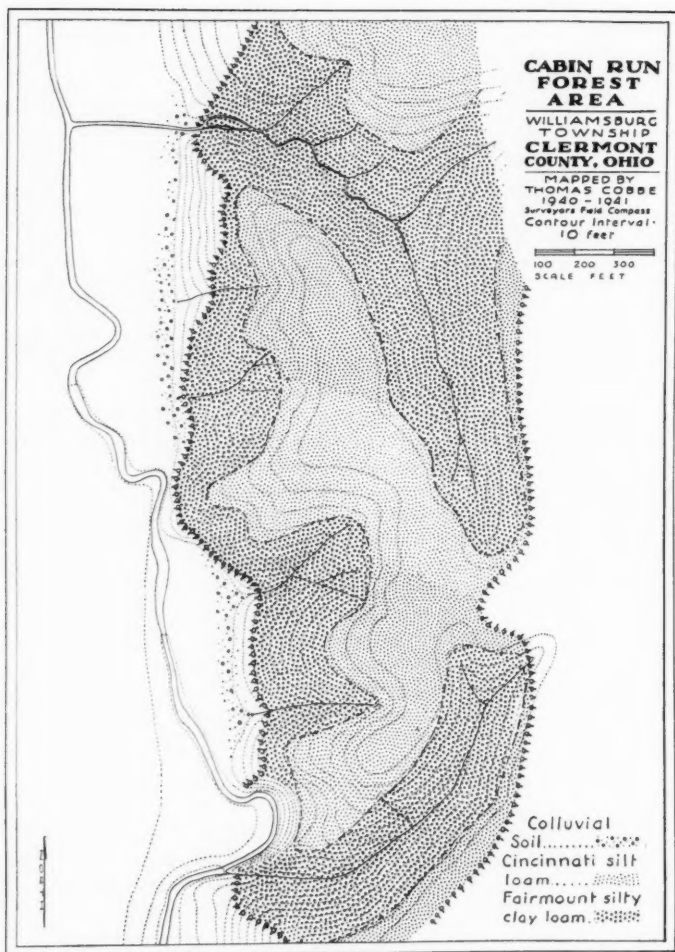


Fig. 1. Soil map. Cabin Run forest area.

Observations and Description of the Vegetation

This paper presents the result of a study from May, 1940 to May, 1941, of the vegetation and habitat factors of this limited forest area in southwestern Ohio. The units of study were natural ones, each of different size and irregular shape. The boundaries, established at the limits of each community, were determined by field observations and selected for study because they obviously marked a contrast in vegetation. The accompanying map (Fig. 2), constructed by the writer with a surveyor's field compass, shows the topographic features, location of stations, and the limits of undisturbed forest.

To Dr. E. Lucy Braun grateful acknowledgment is made for the valuable guidance and criticism which she has given in this study.

MIXED MESOPHYTIC FOREST COMMUNITIES

A general grouping of the communities is made; the interrelations of these will be discussed later. Variation in slope exposure and soil moisture particularly are reflected in these communities.

North Facing Slope Community.—The most mesophytic community with the greatest number of species is found on the northern slopes of the ravines. Seven localities of this community were studied (indicated on the map, Fig. 2, by numbers 11, 12, 13, 14, 33, and 35). *Fagus grandifolia*, *Tilia americana*, *Liriodendron tulipifera*, *Quercus alba*, and *Juglans nigra* (the latter not included in the areas quantitatively studied) are the important species. Seven others occur in the canopy. The accompanying polar graphs (Fig. 3) illustrate the abundance percentage, basal area percentage, and layering of the canopy species in this community.¹ The canopy is dense; below it there are two, and often three, layers. The understory is dominantly *Acer saccharum* often mixed with *Fraxinus americana*; *Fagus grandifolia*, *Tilia americana*, *Quercus alba*, *Ulmus fulva*, *Fraxinus quadrangulata*, *Cornus florida*, *Ostrya virginiana*, and *Carpinus caroliniana* are local or scattered constituents of this layer. *Liriodendron tulipifera* reproduces only in the openings offered by the death of canopy trees.

The shrub layer is composed of *Hydrangea arborescens*, *Benzoin aestivale* and *Dirca palustris*, with young trees of *Fraxinus quadrangulata*, *Acer saccharum*, *Quercus borealis* var. *maxima*, *Quercus alba*, *Carya glabra*, *Carya cordiformis*, *Ostrya virginiana*, *Tilia americana*, *Morus rubra* and *Cornus florida*. *Morus rubra* and *Hydrangea* make dense thickets. In this forest community on well protected and generally steep slopes there is a prolific growth of ferns, mainly *Adiantum pedatum*, *Athyrium pycnocarpon*, *Athyrium*

¹ Polar graphs, used in this paper resemble the phytographs introduced by H. L. Lutz in 1930. Frequency cannot be shown for the species in this study because entire communities were studied in most cases, or entire examples of them. Three concepts are shown on the axes of the polar graphs; these are abundance percentage, basal area percentage (figured on the basis of a unit area of one tenth hectare), and layering of the canopy species. Three layers are represented: canopy, understory, and shrub or young tree layer.

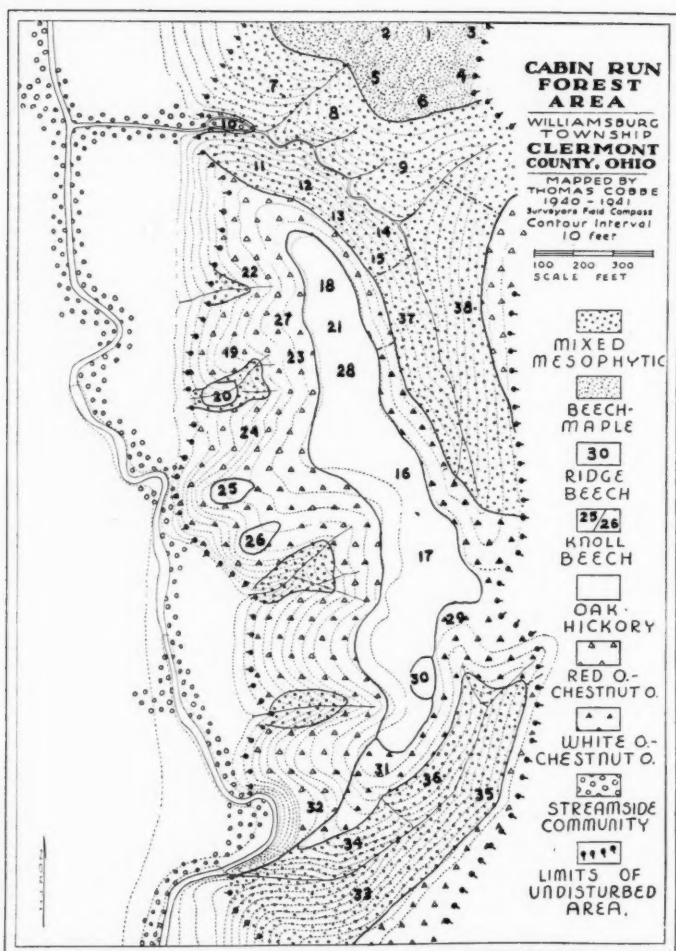


Fig. 2. Forest communities, Cabin Run forest area.

thelypteroides, *Cystopteris fragilis*, *Dryopteris hexagonoptera*, *Polystichum acrostichoides*.²

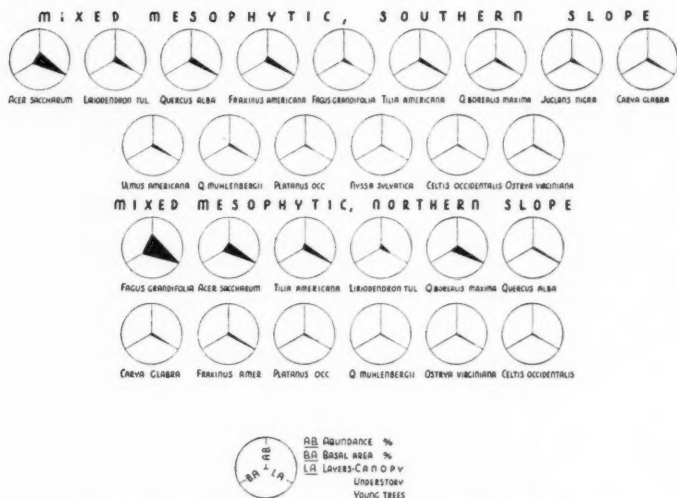


Fig. 3. Polar graphs for the Mixed Mesophytic forest communities.

Characteristic components of the herbaceous layer are:

<i>Adiantum pedatum</i>	<i>Jeffersonia diphylla</i>
<i>Athyrium pycnocarpon</i>	<i>Osmorhiza Claytoni</i>
<i>Athyrium thelypteroides</i>	<i>Oxalis europaea</i>
<i>Cystopteris fragilis</i>	<i>Parthenocissus quinquefolia</i>
<i>Dryopteris hexagonoptera</i>	<i>Phlox divaricata</i>
<i>Polystichum acrostichoides</i>	<i>Podophyllum peltatum</i>
<i>Anemone thalictroides</i>	<i>Polygonum virginianum</i>
<i>Arisaema triphyllum</i>	<i>Polymnia canadensis</i>
<i>Asarum canadense</i>	<i>Ranunculus abortivus</i>
<i>Cardamine Douglasii</i>	<i>Sanguinaria canadensis</i>
<i>Cimicifuga racemosa</i>	<i>Smilacina racemosa</i>
<i>Dentaria laciniosa</i>	<i>Trillium sessile</i>
<i>Erythronium albidum</i>	<i>Trillium Gleasoni</i>
<i>Galium triflorum</i>	<i>Uvularia grandiflora</i>
<i>Geranium maculatum</i>	<i>Viola sororia</i>
<i>Hepatica acutiloba</i>	<i>Viola striata</i>
<i>Hydrophyllum appendiculatum</i>	

This community of the north facing slope, as compared with the opposite slope, shows a later growth and flowering of the spring flora, and delayed development of the tree leaves.

² The nomenclature follows C. C. Deam, 1940.

South Facing Slope Community.—Less dense and mesophytic than the north facing slope community is that of the southerly exposure. The north facing slope canopy is here composed of fifteen species, most of which are important. (Five areas were studied, numbers 7, 8, 9, 34, and 36 on map, Fig. 2). *Acer saccharum* is most abundant, it occurs in all layers; several individuals attain a diameter of over 20 inches. No one species is dominant. *Acer* makes up but 27 percent of the canopy individuals and 24.3 percent of the basal area. Six of the eight important species are represented by an abundance of less than 10 percent. Other important canopy members are *Liriodendron tulipifera*, *Quercus alba*, *Fraxinus americana*, *Tilia americana*, *Juglans nigra*, *Fagus grandifolia*, *Quercus borealis* var. *maxima* and *Carya glabra*. The accompanying polar graphs indicate the relations of these species (Fig. 3).

Layering on the south facing slopes is not conspicuous. The understory is composed of *Acer saccharum*, *Tilia americana*, *Quercus alba*, *Carpinus caroliniana*, *Quercus borealis* var. *maxima*, *Juglans nigra*, *Cornus florida* and *Ulmus fulva*. Each species is locally dominant in the understory. The distribution varies with the minor topographic features. The shrub layer is composed of *Hydrangea arborescens*, *Benzoin aestivale* and young trees of the understory layer. It is well developed only where beech is not a dominant in the canopy.

The herbaceous layer of the south facing slope is nowhere as dense nor as varied as on the north facing slopes, and decreases in density on the upper slopes. Ferns (*Athyrium pycnocarpon*, *Athyrium thelypteroides*, *Dryopteris hexagonoptera*, *Polystichum acrostichoides*) occur in the valley bottom and the lower protected slopes. Grasses (*Diarrhena americana*, *Elymus villosus*, *Leersia virginica*, *Muhlenbergia tenuiflora*) are locally dominant on dried exposed slopes. *Jeffersonia diphylla* forms societies on the upper slopes. Components of the herbaceous layer are:

<i>Athyrium pycnocarpon</i>	<i>Galium triflorum</i>
<i>Athyrium thelypteroides</i>	<i>Geranium maculatum</i>
<i>Botrychium virginianum</i>	<i>Hydrophyllum appendiculatum</i>
<i>Dryopteris hexagonoptera</i>	<i>Jeffersonia diphylla</i>
<i>Polystichum acrostichoides</i>	<i>Leersia virginica</i>
<i>Actaea alba</i>	<i>Luzula echinata</i>
<i>Anemonella thalictroides</i>	<i>Muhlenbergia tenuifolia</i>
<i>Arisaema triphyllum</i>	<i>Oxalis europaea</i>
<i>Aster cordifolius</i>	<i>Parthenocissus quinquefolia</i>
<i>Aster Shortii</i>	<i>Phlox divaricata</i>
<i>Bromus purgans</i>	<i>Polymnia canadensis</i>
<i>Campanula americana</i>	<i>Ranunculus abortivus</i>
<i>Carex blanda</i>	<i>Ranunculus micranthus</i>
<i>Claytonia virginica</i>	<i>Ranunculus hispidus</i>
<i>Dentaria laciniata</i>	<i>Solidago latifolia</i>
<i>Diarrhena americana</i>	<i>Trillium sessile</i>
<i>Elymus villosus</i>	<i>Uvularia grandiflora</i>
<i>Eupatorium coelestinum</i>	<i>Viola sororia</i>
<i>Eupatorium rugosum</i>	

Spring vegetation develops early and imparts a very mesophytic appearance which is lost more rapidly than on the opposing slope.

The polar graphs indicate that both north and south facing slope communities are mixed but in the north facing slope community there are four species that are more important than the other. In the north facing slope community *Fagus grandifolia* seems to be dominant. As the polar graphs show, there is a large number of individuals of beech but a small basal area. This indicates that these individuals are not important in the canopy. The south facing slope community is drier as is shown by the greater abundance of oak and ash, and fewer basswood individuals; the north facing slope is the more mesophytic.

The mixed mesophytic forest shows many habitat variations. In widened valleys one or more species may become dominant. *Fragus grandifolia*, *Acer saccharum*, *Liriodendron tulipifera* and *Tilia americana* may be locally important.³

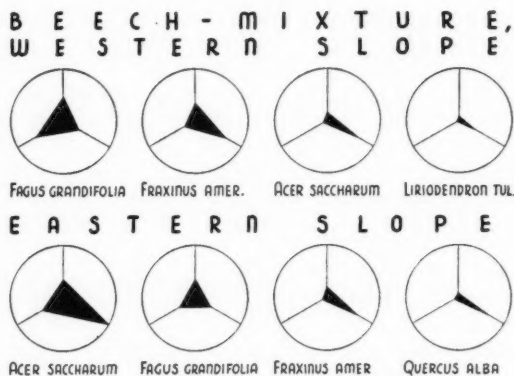


Fig. 4. Polar graphs for the Beech-Mixed forest communities.

In the Cabin Run forest in a wide protected ravine (see map Fig. 2, number 30) *Liriodendron tulipifera*, *Fagus grandifolia* and *Acer saccharum* are the conspicuous canopy constituents (Fig. 5). *Liriodendron* has an abundance of 58.0 percent, and a basal area of 48.7 percent; *Fagus grandifolia* is a conspicuous constituent but is represented only by two large individuals, *Liriodendron* is represented by 11 individuals. The canopy is dense. The understory is composed of *Liriodendron tulipifera* and *Acer saccharum*. Shrubs are lacking and the herbaceous layer includes the same species as the north facing slope.

Beech-Mixed Community.—In the north-south branch ravine, in the northeast part of the study, there are two areas (Fig. 2, numbers 37 and 38), referred to the Beech-Mixed Community because of the obvious dominance of Beech.

³ Such communities were also observed in a comparable forest east of Stonelick Creek and north of U. S. Highway Route 50, in northwestern Clermont County.

It is to be noted that the species here are the five most important ones in the south facing slope community. This then would indicate a decreasing mesophytism which is supported by soil moisture data. *Fagus grandifolia* and *Fraxinus americana* on the western slope have high basal-area percentages in comparison with their abundance (Fig. 4). The same is true on the east

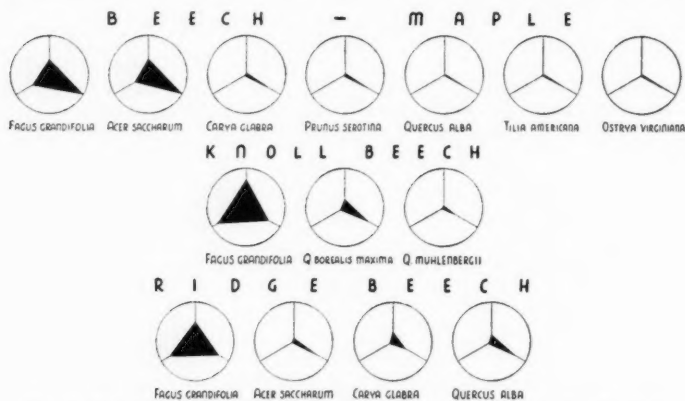


Fig. 5. Polar graphs for the Beech-Maple, Knoll Beech, and Ridge Beech forest communities.

facing slope for *Fagus* and *Acer saccharum*. This indicates that the species are dominant large canopy trees (Fig. 4). The tulip tree on the west facing slope is near the stream. The small number of species, the lack of layering and the kind of herbaceous species impart a drier aspect to the west facing slope.

Layering is not obvious in either area. This is shown in the polar graphs; only one species (*Acer saccharum*) is represented in all layers. The lower part of the ravine has a herbaceous layer including many ferns, resembling the north facing slope herbaceous layer. *Athyrium pycnocarpon*, *Athyrium thelypteroides*, *Dryopteris hexagonoptera* and *Polystichum acrostichoides* are common, making up most of the herbaceous layer in the north end of the ravine. Ferns become less dominant in the southern part. This layer, higher on the slopes and higher in the ravines, is much the same as that of the south facing slope community.

Ridge Beech and Knoll Beech Communities.—Those communities called Ridge Beech and Knoll Beech (Fig. 2, number 25, 26, 30) are similar in physiognomy. Beech is dominant (Fig. 5). In the ridge community it has an abundance of 50.0 percent, and a basal area percentage of 75.5. In the knoll communities, it has an abundance of 72.7 percent and a basal area percentage of 81.5. Other canopy tree species are those of the surrounding communities. In the knoll community, *Quercus borealis* var. *maxima* and *Quercus Muhlen-*

bergii are the only other species. In the ridge community *Acer saccharum*, *Carya glabra* and *Quercus alba* are part of the surrounding White oak and Red oak communities. The canopy in both communities is open; there is no layering. Due to the great exposure to the west winds in the knoll community, much of the leaf litter is blown away and what remains does not decompose rapidly. *Ceratodon purpureus* and *Cladonia* spp. cover this more or less exposed soil.

The herbaceous plants of this community are:

Cardamine Douglasii
Claytonia virginica
Dentaria laciniata
Dodecatheon Meadia

Luzula echinata
Polygonatum biflorum
Prenanthes altissima
Senecio obovatus

Streamside Community.—In the north ravine, an island in the stream supports a forest community which still retains streamside species (Fig. 2, number 10). *Platanus occidentalis* is dominant (52.5 percent abundance, 63.7 percent basal area). Other canopy species are *Acer saccharum*, *Juglans nigra*, *Liriodendron tulipifera* and *Carya glabra* (Fig. 6). There are a few small

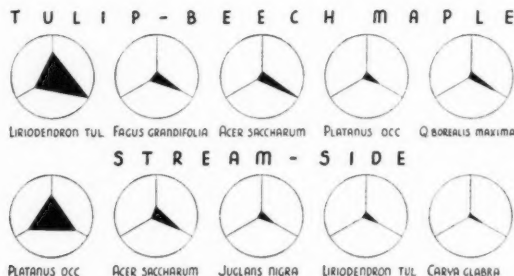


Fig. 6. Polar graphs for the Tulip-Beech-Maple and Streamside forest communities.

trees; west of the island and the area studied, small willows follow the stream. The herbaceous layer is composed of:

Botrychium virginianum
Cystopteris fragilis
Asarum canadense
Claytonia virginica
Dentaria laciniata
Erythronium albidum
Galium triflorum
Impatiens biflora
Impatiens pallida

Jeffersonia diphylla
Lobelia siphilitica
Oxalis europaea
Phlox divaricata
Podophyllum peltatum
Trillium sessile
Viola eriocarpa
Viola striata

OAK-HICKORY COMMUNITIES

The oak communities show a regular pattern of distribution that seems to be related to the slope exposure. The oak-hickory forest type occupies the

driest situations, the ridges (Fig. 2, numbers 17, 18, 21, 28). Red oak and chestnut oak together occupy the exposed, dry west facing slopes in a belt varying in width depending upon the inclination of the slope, the exposure to winds and insolation. This belt surrounds the oak-hickory forest type in these situations. White oak and red oak with several other species are dominant in a belt that is intermediate between the oak-hickory forest and the mixed forest. White oak and beech occur as a transition between the beech-maple forest and the mixed forest or the red oak-chestnut oak forest type.

Oak-Hickory Community.—Along the crest of the north-south ridge there are four areas (Fig. 2, numbers 17, 18, 21, 28) in which oaks and hickories are dominant. The two oak species present together have an abundance of 48.4 percent and a basal area of 43.2 percent (Fig. 7). Other canopy species are *Acer saccharum* and *Fagus grandifolia*. Layering is not obvious; the forest has an open aspect. Understory trees are of the same species as the canopy,

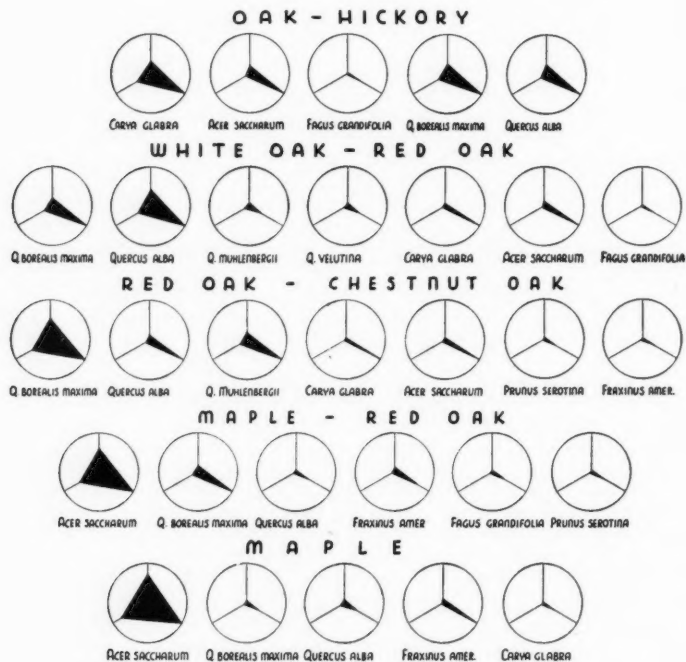


Fig. 7. Polar graphs for the Oak-Hickory, White oak-Red oak, Red oak-Chestnut oak, Maple-Red oak, and Maple forest communities.

except that beech is not present. The same species are represented again in the young tree group. Shrubs are almost lacking and the herbaceous layer is composed of a small number of species. *Claytonia virginiana* shows the greatest density in this forest type, forming a dense carpet in early spring. The herbaceous layer is composed of the following species:

<i>Agrimonia rostellata</i>	<i>Luzula echinata</i>
<i>Agrostis perennans</i>	<i>Panicum dichotomum</i>
<i>Anemonella thalictroides</i>	<i>Phlox divaricata</i>
<i>Claytonia virginiana</i>	<i>Ranunculus micranthus</i>
<i>Dentaria laciniata</i>	<i>Rosa caroliniana</i>
<i>Desmodium rotundifolium</i>	<i>Senecio obovatus</i>
<i>Elymus villosus</i>	<i>Smilacina racemosa</i>
<i>Erythronium albidum</i>	<i>Solidago caesia</i>
<i>Galium circaezans</i>	<i>Solidago ulmifolia</i>
<i>Hystrix patula</i>	

Red Oak-Chestnut Oak Community.—The west slope transition (Fig. 2, numbers 19, 22, 23, 24, 27) is composed of red oak (*Quercus borealis* var. *maxima*), abundance 55.4 percent, basal area 54.5 percent, and chestnut oak (*Quercus Muhlenbergii*), abundance 21.6 percent, basal area 19.7 percent, and five other canopy species (Fig. 7). These are *Quercus alba*, *Acer saccharum*, *Carya ovata*, *Prunus serotina*, and *Fraxinus americana*. Layering is evident; the species of the understory are *Quercus Muhlenbergii*, *Quercus borealis* var. *maxima*, *Acer saccharum*, *Quercus alba*, and *Carya ovata*. Along the sharp angle of the transition between the upland or ridge and the valley slopes, layering is more clearly defined. Here red oak, chestnut oak and hickory form a definite layer. Lower on the slope there is an increase in the amount of *Acer saccharum* in the understory. *Cornus florida*, *Cercis canadensis*, and *Amelanchier canadensis* also occur in the young-tree group. *Parthenocissus quinquefolia* and *Rosa caroliniana* are common constituents of the shrub layer. *Dodecatheon Meadia*, *Claytonia virginiana* and *Phlox divaricata* locally carpet the forest floor. The herbaceous layer is composed of:

<i>Agrimonia rostellata</i>	<i>Krigia Dandelion</i>
<i>Agrostis perennans</i>	<i>Lespedeza violacea</i>
<i>Anemonella thalictroides</i>	<i>Panicum Boscii</i>
<i>Antennaria Parlinii</i>	<i>Panicum dichotomum</i>
<i>Aster Shortii</i>	<i>Phlox divaricata</i>
<i>Cardamine Douglassii</i>	<i>Rudbeckia triloba</i>
<i>Carex blanda</i>	<i>Sedum ternatum</i>
<i>Claytonia virginiana</i>	<i>Senecio obovatus</i>
<i>Dentaria laciniata</i>	<i>Silene stellata</i>
<i>Desmodium pauciflorum</i>	<i>Solidago caesia</i>
<i>Desmodium rotundifolium</i>	<i>Solidago nemoralis</i>
<i>Dodecatheon Meadia</i>	<i>Solidago ulmifolia</i>
<i>Elymus villosus</i>	<i>Tradescantia virginiana</i>
<i>Erythronium albidum</i>	<i>Trillium sessile</i>
<i>Fraseria carolinensis</i>	<i>Uvularia grandiflora</i>
<i>Galium circaezans</i>	<i>Vicia caroliniana</i>
<i>Houstonia purpurea</i>	<i>Viola rostrata</i>
<i>Hystrix patula</i>	<i>Viola sororia</i>

White Oak-Red Oak.—The white oak-red oak forest type (Fig. 2, num-

bers 29, 31) is composed of seven canopy species (Fig. 7). White oak is dominant with an abundance of 43.0 percent and a basal area of 27.9 percent. Red oak has an abundance of 19.6 percent, and a basal area of 24.4 percent. The other canopy members are *Quercus Muhlenbergii*, *Quercus velutina*, *Acer saccharum*, *Carya ovata*, and *Fagus grandifolia*. In this forest type, as in the oak-hickory type, there is no prominent layering. Young trees constitute the shrub layer. Maple reproduction here is not as dense as it is in the more mesophytic communities. The herbaceous layer is grassy and more mesophytic in aspect than that of the oak hickory or the red oak-chestnut oak forest types; it is composed of:

<i>Agrimonia rostellata</i>	<i>Jeffersonia diphylla</i>
<i>Agrostis perennans</i>	<i>Lespedeza violacea</i>
<i>Anemonella thalictroides</i>	<i>Luzula echinata</i>
<i>Cardamine Douglassii</i>	<i>Panicum Boscii</i>
<i>Carex blanda</i>	<i>Panicum dichotomum</i>
<i>Claytonia virginiana</i>	<i>Phlox divaricata</i>
<i>Dentaria laciniata</i>	<i>Senecio obovatus</i>
<i>Desmodium pauciflorum</i>	<i>Silene stellata</i>
<i>Elymus villosus</i>	<i>Solidago caesia</i>
<i>Erythronium albidum</i>	<i>Solidago nemoralis</i>
<i>Frasera carolinensis</i>	<i>Solidago ulmifolia</i>
<i>Galium circaezans</i>	<i>Trillium sessile</i>
<i>Houstonia purpurea</i>	<i>Uvularia grandiflora</i>
<i>Hystrix patula</i>	

Two variations in the oak-hickory forest occur. These are the result of disturbance. The one (Fig. 2, number 32) is the result of sapping away of the cliff by Cabin Run. By the progressive retreat of this cliff the large trees were removed. Maple and red oak have replaced them (Fig. 7, Maple-Red oak). On the ridge (Fig. 2, number 16), windfall has downed the trees in a narrow passage across the oak-hickory forest. Maple occurs in this disturbed area (Fig. 7, Maple).

Habitat Factors

The variations in the climax forest recognized within this area require an explanation. On the basis of soil characters in the Cabin Run area certain correlations of the forest types and the habitat will be made. The hydrogen-ion concentration, soil-texture and moisture studies are used because their variations correspond to the distribution of vegetational patterns. The available moisture probably is a controlling factor in the distribution of communities. The other factors probably do not control the vegetation but can be used as indicators in the study.

Soil Moisture.—Soil moisture data were collected at 13 stations for 12 consecutive weeks from June 29 to September 22, 1940. Available moisture and total moisture were measured. Precipitation, evaporation, runoff, percolation, soil texture, plant cover and insolation are all factors affecting the amount of available moisture. Soil moisture is here used as a measure of the other factors.

Several features are to be noted concerning the available moisture studies

(Fig. 8). There are two major groups in the 13 stations studied. One of these has a lower percentage of available moisture and shorter periods in which it is available (Fig. 8, numbers 1, 3, 4, 4a, 5, 6, and 7). After each period of precipitation there was a rapid rise in the available moisture followed by a rapid

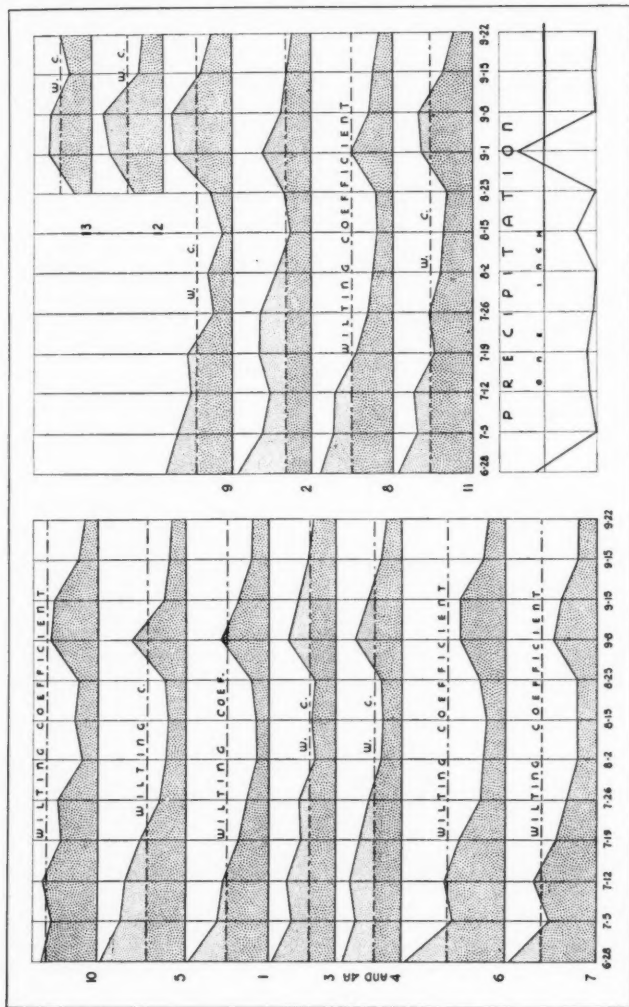


Fig. 8. Soil moisture. Cabin Run forest area.

decline. This may be explained by the fact that these stations were located on ridges or on knolls. Loosely consolidated soil, relatively unprotected by vegetation, on essentially flat locations allows rapid percolation. Exposure to sunlight and wind causes rapid evaporation. The "A" horizon rapidly loses its available moisture. This area, with a lower percentage of soil moisture, supports oak-hickory, white oak-red oak, red oak-chestnut oak, ridge beech and knoll beech communities.

A second group of soil moisture stations shows higher percentages of, and longer periods of available moisture (Fig. 8, numbers 2, 8, 9, 11, 12, and 13). This is explained by the location of these stations in ravines. These stations are located on the Fairmount silty clay loam. The humus layer is of the mull type. The "A" horizon is loose and friable because of the incorporation of a large amount of organic material. Evaporation from this soil type is low and the movement of ground water does not deplete the supply which is maintained by drainage from higher ground. The graphs (Fig. 8, numbers 2, 8, 9, 11, 12, and 13) show that the soil of these ravine stations increased in total moisture for a week or more after any increase is shown for the upland stations. There may be a greater and extended period of available moisture (Fig. 8, numbers 12 and 13). This group of soils supports mixed mesophytic, beech-mixed, tulip-beech-maple, and streamside communities.

A third type of soil moisture availability may be distinguished; this example has a typical valley or mixed forest distribution of available moisture periods and emphasized effect of rain (Fig. 8, number 10). It is located on the upland in the beech-maple community. The canopy is dense and the soil is protected by leaf litter and a dense growth of maple seedlings.

Soil Acidity.—The soil-acidity study is based on 180 determinations evenly distributed in the area. Determinations were made with a calomel cell-quinhydrone electrode hydrogen-ion concentration indicator. These 180 samples may be grouped according to hydrogen-ion concentration (Fig. 9B). The greatest alkalinity is found in the ravines (pH 7.4 in the north ravine; pH 8.1 and pH 8.3 in the south ravine), in the mixed mesophytic forest communities, and the greatest acidity on the ridges and uplands. The most acid sample (pH 4.1) was found on the oak ridge and the most alkaline (pH 8.3) was found in the south ravine.

Correlation of Vegetation and Habitat Factors.—Considering three habitat factors, namely, soil type, soil acidity, and soil moisture, certain relations can be established between their spatial limits of variation and plant communities. There is no claim made that these factors individually or collectively are entirely responsible for community distribution. In part, at least, they are affected by the occupying vegetation.

On the Cincinnati silt loam, the upland soil type, are found oak-hickory, white oak-red oak, red oak-chestnut oak, ridge beech, knoll beech and beech-maple communities. On the Fairmount silty clay loam are found the mixed mesophytic, beech-mixed and tulip-beech-maple communities.

Those areas, with a particularly acid "A" horizon, the ridges and uplands, (Fig. 9B) support oak-hickory communities, ridge beech and knoll beech communities. The red oak-chestnut oak community is essentially co-extensive with the zone of pH 5 (including part of the pH 4 zone on the west of the area) (Fig. 9, B and C). The white oak-red oak community continues in this zone on the north, east and south facing slopes. White oak-beech transition community is found on the west facing slopes in the northwest portion of the area. The oak-hickory forest is located on the most acid zone (pH 4). The mixed communities occur on soils of pH 5.8 to 8.3. These zones follow the contours of the ravines (Fig. 9B).

If the soil moisture is considered in terms of the periods of availability, certain zones can be established (Fig. 9A). The basis for the soil moisture map is the number of weeks of available moisture during a 10 week period (June 29 to Sept. 8, 1940).

Classification of Communities

Within the limits of the Cabin Run forest there are at least seven distinct variations in the composition of the deciduous forest. They are characterized by the number and kind of canopy dominants, the presence or absence of layering and the character of the herbaceous layer. All the communities here

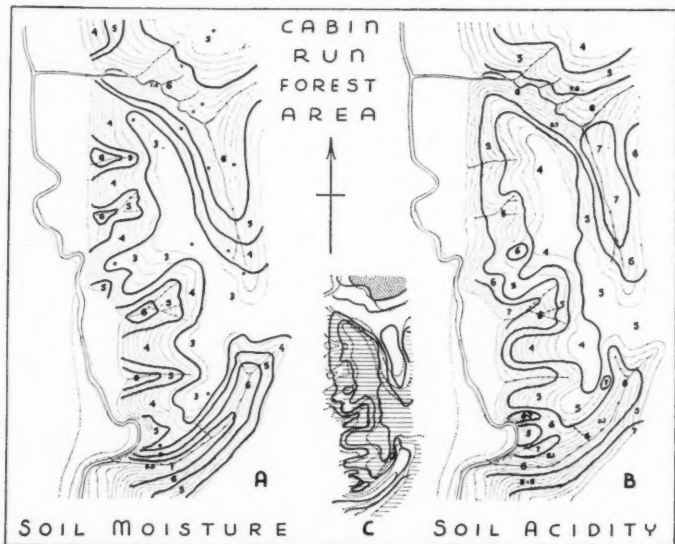


Fig. 9. Habitat factors. Cabin Run forest area. a, Soil moisture; b, Soil acidity; c, Forest communities, horizontal lines indicate extent of the Oak-Hickory communities, stipple indicates the extent of the Beech-Maple forest community.

recognized are stable; there is no evidence of succession except the return to the dominant vegetation from very local subseries.

There is no doubt that there is an oak-hickory forest occupying the ridges and dry uplands. The recognition of this community becomes more difficult as the habitat becomes more mesophytic. Under these conditions the number of dominants, especially in the understory, increases. The canopy in the oak-hickory and the mixed mesophytic communities influences the lower layers. The herbaceous layer in the former is depauperate in species and individuals, that of the latter is rich and includes many ferns. The mixed forest occupies neutral or alkaline soil covered with a mull layer; the oak-hickory community occupies acid soil with a mor humus layer.

The oak-hickory forest is a physiographic climax or subclimax. Its limitation of extent prohibits its classification as a climax. The variations of this forest type are due to the same causes as the variations in the mixed mesophytic forest. The red oak-chestnut oak transition extends farther down the west facing slope than the others. This zone becomes a narrow transition on the north facing slopes. White oak-red oak forms the transition zone on the south facing slopes.

The mixed mesophytic forest is the climax. In this area it is made up of several variants just as in the oak-hickory forest. It occupies all the protected slopes, ravines and mesophytic uplands. The aspect of all the mesophytic communities is the same. The polar graphs (Fig. 3) show that there are many species of equal importance. This forest is not as complex as that in the Kentucky mountains (Braun, 1940, p. 236). In the mixed forest of the Cabin Run area there are six species (*Acer saccharum*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Tilia americana*, *Juglans nigra*, *Quercus alba*) that are nearly always present and may be locally and individually dominant. These compose about 80 percent of the canopy trees. Beech is a species with a very wide range of habitat requirements. It is locally dominant in the ravines, on knolls, ridges, and moist uplands. In the last situation it is associated with maple. The northern slope communities include more beech than the south facing slope but there is a typical mixed character. The south facing slopes appear drier because of an increase in maple and ash, less dense subcanopy layers and lack of spleenworts in the herbaceous layer. In the mixed forest white oak is more important on the south facing slopes than on the north facing slopes. Red oak extends into the mixed mesophytic forest but is not here a characteristic part of it. East and west facing slopes show fewer canopy dominants. These support beech-mixed communities.

There are eleven or more variants distinguishable in this area, but all cannot be referred to the canopy types described here. Some of these are intermediate between the types here recognized, i.e., are transitional communities. A great amount of variation occurs indicating the differences in environment and specific requirements. These variations of the forest may be referred to as lociations (Clements, 1936).

The area as a whole is composed of two elements; oak-hickory, a subclimax or physiographic climax. The Cabin Run forest is far from the central region

of the mixed mesophytic forest and close to its northern limit. It is genetically younger and less complex than the central part of the association, the Cumberland Mountains (Braun, 1941).

Summary

This paper deals with a study of variations in the climax forest in Clermont County, southwestern Ohio. Studies of entire communities were made. These reflect the variations of the forest due to the differences in slope exposure, soil moisture, and interaction of the vegetation. All protected ravine slopes support some variant of the climatic climax, the mixed mesophytic forest. As exposure increases, oaks become more important, forming oak transition communities, and finally ridges support the oak-hickory forest.

The delimitation of communities is based upon canopy composition, and density of lower layers. The boundaries are placed where the influence of the canopy is reflected in the herbaceous layer. The line is found to approximate certain limits of acidity and available moisture.

The oak-hickory communities are composed of red oak, white oak, chestnut oak and hickory dominants. The number of variants is small; these are distinctly transitional.

The mixed mesophytic forest is represented by several variations and transitional communities. There are six important species and as many as fourteen additional species.

The Cabin Run forest, near the northern limit of the mixed mesophytic association, is generally younger and less complex than the central portion.

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The Distribution of *Adenostoma sparsifolium*

Lois H. Marion

Introduction

The distribution of plants offers a rich field for study, and such a species as *Adenostoma sparsifolium* Torr. presents a particularly complex and interesting problem because of its restricted and widely separated areas of occurrence. However, it is not the purpose of this paper to attempt an intensive study of the species, but merely to present the geographic boundaries of its distribution, as well as records of altitude, slope exposure, and associated species, in the hope that the information may provide the basic data for such a study.

A. sparsifolium is a slender shrub, in some instances a small tree, from 3 to 15 or even 20 feet high. Its numerous stems rising from a single root system are devoid of foliage for some distance above the ground (Pl. 2, C). Thin red bark peels away from the stems in ragged shreds, giving to the shrub its common name redshanks.¹ Linear, glandular-dotted, pale green leaves are thinly scattered along the branchlets, forming tufts of foliage at the ends of the branches. Yellow-green, feathery branches set this species off sharply from the dark-colored chamise (*A. fasciculatum* H. & A.), its most frequent associate. (For detail of foliage and bark see Pl. 2, A and B.)

This species was first collected in 1846 by Emory near Warner's ranch in San Diego County.

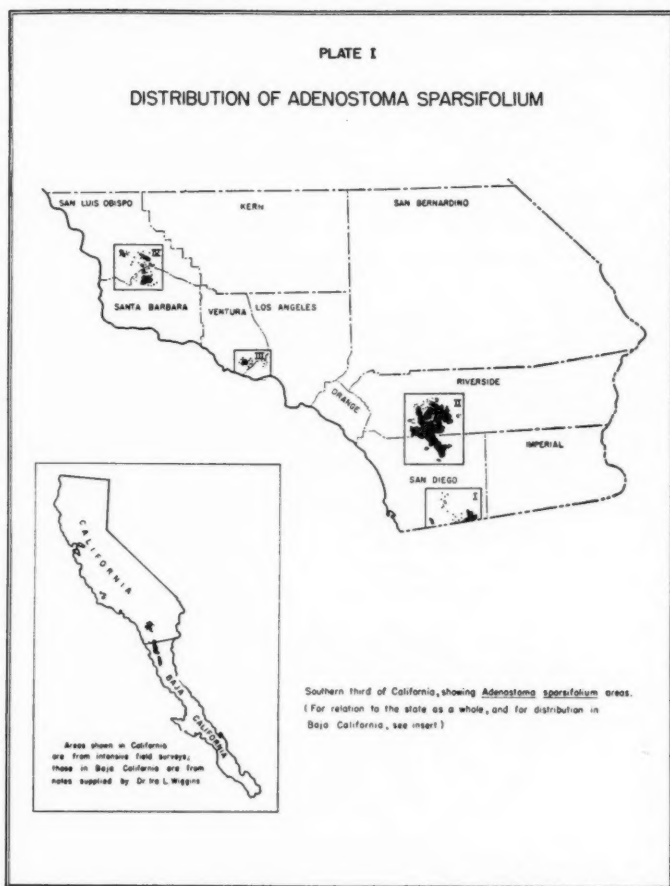
It is one of a group of plants typically belonging to the southern California flora that have relict northern outposts in the South Coast Ranges and elsewhere in central California. In a recent paper, Axelrod² interprets these as "relicts of the early Pliocene invasion of west-central California by the Sierra Madresan Flora. Their distribution suggests that while a portion of the Sierra Madresan Flora was eliminated in late Pliocene time, certain woody plants of southern derivation were able to persist in compensatory sites in central California many miles north of their normal ranges as established today."

Range

A. sparsifolium ranges from northern Baja California to the South Coast Ranges of California, as shown on the accompanying map (Pl. 1). Its recorded

¹ It is also called "ribbon wood."

² Chaney, R. W., D. I. Axelrod, and C. Condit. Late Tertiary Floras of California and Oregon. (Chapter 5. The Mulholland Flora. D. I. Axelrod.) (Geol. Soc. Amer. Spec. Paper. In press.)



distribution in California has been taken from vegetation type maps³ prepared by the Forest Survey Division of the California Forest and Range Experiment Station. The areas shown on Plate 1 represent scattered but closely adjacent

³ These show the distribution of natural plant associations on U. S. Geological Survey topographic quadrangles, each association being defined by its dominant species. The dominants consist of those species forming 20 percent or more of the total vegetation cover in associations that are wholly herbaceous, shrubby, or arborescent, or 20 percent or more of its respective class in composite associations. (See Wieslander, A. E. A vegetation type map of California. Madroño, 3:140-144, 1935.)

stands in which this species makes up 20 percent or more of the vegetation. Comparable data are not available for Baja California, so that the distribution shown on the map is necessarily more generalized for that area.

*Baja California.*⁴—The southern California flora extends into the northwestern section of the peninsula of Baja California. *A. sparsifolium*, which is a constituent of this flora, ranges southward from San Diego County, California, in a narrow belt along the seaward slopes of the Sierra Juarez and Sierra San Pedro Mártir to a point about 30 miles south of the seacoast village of San Quintín. According to Dr. Wiggins:

The distribution is not continuous, for there are places where it drops out for a few miles and then reappears. . . . It is not found in the Valle de la Trinidad, which lies between the southern end of the Sierra Juarez and the northern end of the San Pedro Mártir. This is the largest gap and is about 10 or 15 miles wide. As I have observed it, the shrub is pretty well confined to soil of granitic origin and always to areas in which the drainage is very good.

California.—The distribution of *A. sparsifolium* is discontinuous in California, occurring in four distinct sections (Pl. 1). The southernmost (shown on the map as Region I) is in southeastern San Diego County, thence extending into Baja California. There are large stands near the eastern limit of the species, which is about 3 miles west of Jacumba. In widely scattered areas it extends northwestward to within about 6 miles of Descanso.

In Region II it grows luxuriantly from the lower slopes of the San Jacinto Mountains southward to Volcan Mountain, and to some extent in the ranges bordering the desert (Santa Rosa Mountain and Little Pinyon Flat). This region may be considered its present center of distribution, since 81 percent of the total acreage of *A. sparsifolium* occurs here, where it is one of the predominant species over a large area (237,080 acres).

The species was not recorded for the two northerly regions until recent years when observations and collections made by vegetation type survey crews extended the known range. Region III, in the Santa Monica Mountains, contains a small, isolated area in southeastern Ventura County at the Los Angeles County boundary, and several scattered areas near the coast in southwestern Los Angeles County. This is the only locality in which *A. sparsifolium* is known in the immediate vicinity of the coast.

Region IV is in north-central Santa Barbara County and southern San Luis Obispo County. One large area lies north and northeast of Manzanita Mountain, but its most extensive development is to be found north of the Cuyama River from Gypsum Canyon westward to the base of Los Machos Hills. The northernmost station recorded for *A. sparsifolium* is a collection from $3\frac{3}{4}$ miles east-northeast of Pozo, San Luis Obispo County, where it occurs in an *A. fasciculatum*-*Ceanothus cuneatus* association, on a northeast slope at an altitude of 2,100 feet. The specimen (Hendrix 285—VTM

⁴ The author is indebted to Dr. Ira L. Wiggins of Stanford University for notes on the distribution of this species in Baja California.



PLATE 2.—*Adenostoma sparsifolium* in the South Coast Ranges: A. Detail of foliage; B. shreddy bark; C. slender, leafless stems.

Herbarium) collected by a member of a type map crew bears the note: "This 2-acre stand is probably the northern limit of its range."

Altitude and Slope Exposure

In Region I *A. sparsifolium* ranges from 2,500 to 4,000 feet, with the majority of the localities from 3,500 to 4,000 feet. In Region II most of its area is within the altitudes 3,000 to 5,500 feet, but it occurs as low as 1,500 and as high as 7,000 feet. At the north it grows at lower elevations, from 1,000 to 2,500 feet in Region III and from 750 to 3,750 (mostly 1,500 to 3,000 feet) in Region IV.

Redshanks does not seem to show any marked relation to slope exposure. The areas on the type map indicate that it is fairly well distributed over the various slopes. This also holds true on sample plots⁵ taken during the mapping.

Climate

All four regions are in a climatic zone having dry summers and rainy winters. The mean annual precipitation varies through the range of redshanks from less than 15 inches to 35 inches but averages about 15 to 20 inches. In Region I the largest stands are in a zone of 15 to 20 inches; others are scattered through areas having from 20 to 30 inches, especially in the Cuyamaca Mountains. Region II has a wide variation in rainfall. Most of the *A. sparsifolium* in that region occurs in localities having 15 to 25 inches of rainfall, but some of it ranges into areas having less than 15 inches, and certain stands are on mountain slopes having as much as 35 inches. The northern regions (III and IV) have from 15 to 20 inches.⁶

The relationship between the distribution of this species and temperature is unknown, as none of the stations recording temperature data are close enough to the *A. sparsifolium* areas to be of value.

In Regions I and II redshanks occupies the foothills of the inner ranges, the San Jacinto and Cuyamaca Mountains, which are sheltered from direct ocean winds by intervening ranges. In the San Jacinto Mountains it extends southeastward onto the desert slopes, where it is found mainly on the western side of Santa Rosa Mountain. In the northern Santa Barbara and southern San Luis Obispo Counties it occurs on the intermediate ranges between the coastal hills and those bordering the upper San Joaquin Valley. Its only approach to the coast is in the Santa Monica Mountains, and here it is usually found on the inner slopes rather than the coastal side.

⁵ Sample plots are taken simultaneously with the mapping of vegetation types. The plots cross section all types for such details as species composition, stand density, depth of leaf litter, and other data. Each consists of a rectangular 1/10 acre in size, visually subdivided into mil-acre squares (6.6' × 6.6'). Species dominating each of these squares are recorded, while all other species present are separately designated.

⁶ Rainfall data for Regions I and II from unpublished precipitation map of southern California compiled by A. Simontacchi, Calif. Forest and Range Expt. Sta.; for Regions III and IV from U. S. Dept. Agr. Weather Bur., Climatic Summary of the U. S., Sec. 17, Central Calif. 1934, and Sec. 18, S. Cal. and Owens Valley, 1932.

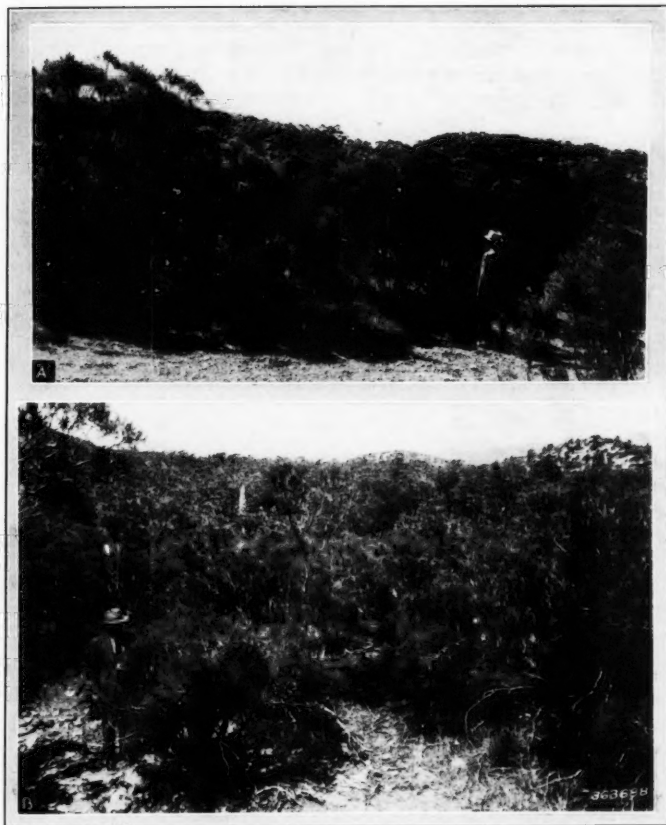


PLATE 3.—*Adenostoma sparsifolium*: A. South Coast Ranges; B. San Jacinto Mountains.

Soil

This species, like its relative, chamise, grows in rocky areas, on coarse gravelly or sandy soils. In the southern part of its range (Regions I and II), the underlying formation is mostly granitic rock.⁷ In general the soil is rather shallow, and the ground is typically strewn with boulders. In the northern area of its distribution (Regions III and IV) the soil is largely of sandstone origin. The general appearance of the country is similar to the southern area, with scattered boulders and coarse, sandy soil. Near its northern limit redshanks is found on a loosely-cemented, fossiliferous sandstone of Miocene marine origin.

Relation to Fire

A large number of the areas in which *A. sparsifolium* occurs shows effects of fire. The shrub is highly inflammable but is able to survive fires by sprouting from a burl after the portion of the plant above ground has been destroyed (Pl. 4). Sometimes several large treelike trunks may spring from a single root crown. The burl formations are not a result of fire, but a characteristic of the species, developing even in unburned areas.

Economic Value

The burls often grow to considerable size and might be a valuable substitute for brier burl in the manufacture of smoking pipes. The best ones for commercial use would be those from areas protected from fire, which may damage the wood of the burl. One block mill, located in southern California has used the burls of redshanks for pipe blocks, but the operator stated that with his type of equipment he could not work the wood profitably, as it was too hard. However, a further investigation of their commercial possibilities would be desirable, since some fine burls are to be found in the South Coast Ranges area.

Vegetation Types

A. sparsifolium occurs as a dominant species (that is, one forming at least 20 percent of the shrub species in the type) in the following vegetation types recognized by the Vegetation Type Survey in California: sagebrush, chamise chaparral, chaparral, semidesert chaparral, woodland—chaparral, and piñon. The distribution by these types is shown in Table 1, which indicates that *A. sparsifolium* rarely occurs outside the chaparral types. By far its most common occurrence is in the chamise-chaparral type, an association of shrubs, in which chamise (*A. fasciculatum*) is one of the dominant species. Chamise chaparral makes up nearly 87 percent of the total area in which *A. sparsifolium* is present as a dominant species. On only about 3 percent of the total area does *A. sparsifolium* occur in pure stands.

⁷ Geological map of the State of California, State Mining Bur., 1916; Geologic map of California, Sheet No. VI. South. Sec. (1st ed.), Div. Mines. 1938.

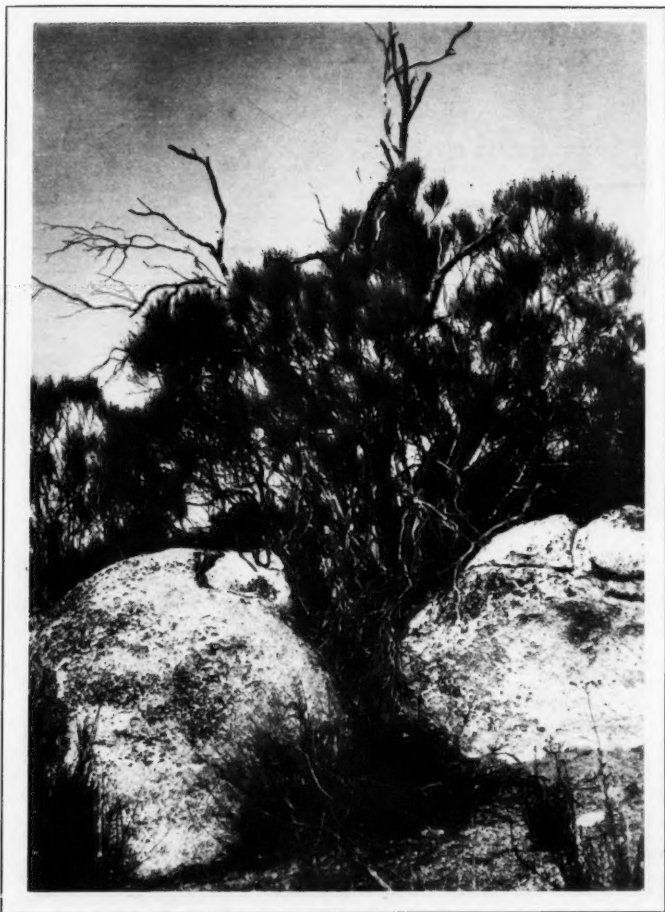


PLATE 4.—Fire-killed stems of *Adenostoma sparsifolium* projecting above the new growth from the same root crown. San Jacinto Mountains.

TABLE 1.—Area of different vegetation types in which *Adenostoma sparsifolium* is present as one of the dominant species.*

Vegetation type	Region †				Total	
	I	II	III	IV	Acres	Percent
Sagebrush			60	40	100	.03
Chamise chaparral	21,450	204,290	5,020	21,840	252,600	86.60
Chaparral	4,190	30,310	1,130	860	36,490	12.51
Semidesert chaparral		500			500	.17
Woodland-chaparral	30				30	.01
Piñon		1,980			1,980	.68
Total	25,670	237,080	6,210	22,740	291,700	100.00
Percentage of total area	9	81	2	8	100	

* Obtained from planimeter figures for the areas in which *A. sparsifolium* is shown on the vegetation type map.

† See Pl. 1.

Associated Species

Associations making up the greater part (over 75 percent) of the *Adenostoma sparsifolium* area for each region are as follows:

Region I	{ <i>Adenostoma fasciculatum</i> — <i>A. sparsifolium</i> — <i>Ceanothus Greggii</i> Gray var. <i>perplexans</i> (Trel.) Jepson <i>A. fasciculatum</i> — <i>A. sparsifolium</i> — <i>Quercus dumosa</i> Nutt.
Region II	{ <i>A. fasciculatum</i> — <i>A. sparsifolium</i> <i>A. fasciculatum</i> — <i>A. sparsifolium</i> — <i>C. Greggii</i> var. <i>perplexans</i>
Region IV	{ <i>A. fasciculatum</i> — <i>C. cuneatus</i> (Hook.) Nutt.— <i>A. sparsifolium</i> <i>A. fasciculatum</i> — <i>A. sparsifolium</i> — <i>Salvia mellifera</i> Greene <i>A. fasciculatum</i> — <i>A. sparsifolium</i>

In Region III 10 different associations make up 75 percent of the total, but these are mainly combinations of five species, *A. fasciculatum*, *A. sparsifolium*, *C. megacarpus* Nutt., *Arctostaphylos glandulosa* Eastw.,⁸ and *C. spinosus* Nutt.

A list of all species abundant enough to be recorded on the vegetation type map follows. These are species that make up 20 percent or more of the associations in which *A. sparsifolium* occurs as one of the dominants. Three groups may be designated: xxx—where the species listed is present on 60 to 100 percent of the total area of *A. sparsifolium* distribution in the respective regions, xx—from 20 to 60 percent, x—less than 20 percent (except for two

⁸ The name *Arctostaphylos glandulosa* is here used to represent all species of the *A. tomentosa*—*A. glandulosa* complex.

species in Region III, all in this group are less than 10 percent). The species are arranged in order of abundance.

Region I

<i>Adenostoma fasciculatum</i>	xxx
<i>Ceanothus Greggii</i> var. <i>perplexans</i>	xx
<i>Quercus dumosa</i>	xx
<i>Prunus ilicifolia</i>	x
<i>Arctostaphylos pungens</i>	x
<i>Ceanothus leucodermis</i>	x
<i>Quercus agrifolia</i>	x

Region III

<i>Adenostoma fasciculatum</i>	xxx
<i>Ceanothus megacarpus</i>	xx
<i>Ceanothus spinosus</i>	x
<i>Lotus scoparius</i>	x
<i>Arctostaphylos glandulosa</i>	x
<i>Salvia mellifera</i>	x
<i>Rhus laurina</i>	x
<i>Ceanothus crassifolius</i>	x
<i>Quercus dumosa</i>	x
<i>Ceanothus oliganthus</i>	x
<i>Cercocarpus betuloides</i>	x
<i>Encelia californica</i>	x
<i>Helianthus gracilentus</i>	x

Region II

<i>Adenostoma fasciculatum</i>	xxx
<i>Ceanothus Greggii</i> var. <i>perplexans</i>	xx
<i>Arctostaphylos glandulosa</i>	x
<i>Quercus dumosa</i>	x
<i>Cercocarpus betuloides</i>	x
<i>Ceanothus crassifolius</i>	x
<i>Arctostaphylos glauca</i>	x
<i>Arctostaphylos pungens</i>	x
<i>Quercus Wislizenii</i> var. <i>frutescens</i>	x
<i>Garrya Veatchii</i>	x
<i>Pinus monophylla</i>	x
<i>Quercus chrysolepis</i> (scrub)	x
<i>Ceanothus cuneatus</i>	x

Region IV

<i>Adenostoma fasciculatum</i>	xxx
<i>Ceanothus cuneatus</i>	xxx
<i>Salvia mellifera</i>	xx
<i>Salvia leucophylla</i>	x
<i>Lotus scoparius</i>	x
<i>Eriogonum fasciculatum</i>	x
<i>Arctostaphylos glauca</i>	x
<i>Arctostaphylos glandulosa</i>	x
<i>Quercus dumosa</i>	x
<i>Cercocarpus betuloides</i>	x
<i>Ceanothus leucodermis</i>	x
<i>Yucca Whipplei</i>	x

It is evident that *Adenostoma fasciculatum* and *Quercus dumosa* occur as associated dominants in all four regions. Common to both the southern (I and II) and northern (III and IV) areas are *A. fasciculatum*, *Arctostaphylos glauca*, *A. glandulosa*, *A. pungens*, *Ceanothus cuneatus*, *C. crassifolius*, *C. leucodermis*, *Cercocarpus betuloides*, and *Q. dumosa*. This does not imply that the other species are restricted to the regions in which they are listed; they did not occur elsewhere with *A. sparsifolium* in sufficient quantity to be mapped as one of the dominant species. Examples are *Eriogonum fasciculatum*, *Lotus scoparius*, *Salvia mellifera*, and *Yucca Whipplei*, which occur on sample plots for all four regions. The range of only one of the species listed, *C. Greggii* var. *perplexans*, is restricted to southern California. Three species occur from the South Coast Ranges south into coastal southern California but do not occur in Regions I and II, *Ceanothus spinosus* and *Salvia leucophylla* from San Luis Obispo County southward, and *Ceanothus megacarpus* from Santa Barbara County southward.

One hundred and thirty-seven sample plots were taken in associations in which *A. sparsifolium* was present as a dominant. Ninety-one species were

listed on these plots as associated species, including both dominants and others. The more important, omitting those already included in the foregoing lists of dominant species, are given below. They represent 7 species found on more than 10 percent of the sample plot sheets.

Artemisia tridentata (Regions I and II only)
Eriophyllum confertiflorum
Pholonia arbutifolia
Paeonia Brownii
Rhamnus crocea var. *ilicifolia*
Rhus ovata
Yucca mohavensis (Regions I and II only)

For more detailed information on the distribution of *A. sparsifolium*, the vegetation type maps⁹ may be consulted. On these maps the various associations may be studied with reference to their exact geographic boundaries, associate species, and their relation to altitude and slope exposure.

⁹ The Vegetation Type Maps of California, published on U. S. Geological Survey quadrangles, are available from the University of California Press, Berkeley.

A Few Lichens from Indiana

Albert W. C. T. Herre

The lichen flora of Indiana has been but little collected or studied, if one may judge by the published references to it. There are but three papers known to me which mention them, all partial and very incomplete lists. L. M. Underwood enumerated thirty species in his "List of Cryptogams at present known to inhabit the State of Indiana." This appeared in the Proceedings of the Indiana Academy of Science for 1893. A part of Lake County, Indiana, was included in the area reported upon by W. W. Calkins in his "Lichen Flora of Chicago and Vicinity," Chicago Academy of Sciences Bulletin No. 1, 1896. However I cannot find that Calkins specifically named any lichen as occurring in Lake County. In the Proceedings of the Indiana Academy of Science for 1918 Bruce Fink and Sylvia C. Fuson presented a paper entitled "Ascomycetes new to the flora of Indiana." This paper named 57 species not previously reported from Indiana, and includes two species which thus far are only known from Montgomery County. The Fink-Fuson collection was made by the authors during July, August, and September, 1917, in the following counties: — Franklin, Hendricks, Montgomery, Parke, Tippecanoe, and Union.

Recently Dr. Winona H. Welch, professor of botany at DePauw University, submitted to me a small collection of lichens obtained by her from a few localities, together with a few other specimens without data that she found in the herbarium of DePauw University. Most of the specimens were collected in the woods along the North Fork of the Muscatatuck River, one-half mile north of Vernon, Jennings County. To avoid repetition they will be referred to as being from north of Vernon. Others collected along the Muscatatuck River east of Vernon will be listed simply as from east of Vernon. The numbers preceding the names of species are numbers in Dr. Welch's herbarium.

With one example the species are all common and widespread. The exception is *Physcia virella*. The only previous record from the United States is from Michigan. There is no question that proper collecting of lichens in Indiana would bring to light a large number of species as yet unknown from the state, as well as some not yet recorded from the Ohio Valley. The southern half of Indiana was well wooded and abounded in rocky hills when I knew it and bicycled over it nearly forty-five years ago, and I am sure that favorable habitats for a great variety of lichens are still abundant and widespread. Dr. Bouly de Lesdain, of Dunkerque, France, has shown what can be discovered among sand dunes, and it is certain that many lichens could be made known in the same way in Indiana. From the sand dunes of Lake Michigan to Jug Rock and Lost River, from the "Greenbrier Mountains" of the Wyandotte Cave region to the Wabash swamps of Vincennes, keen-eyed students should collect the lichens of soil, rocks, and trees. No other group of plants illustrates the problems of ecology better or lends itself more readily to physiological experimentation, and no other group is so neglected.

- 7441 and 7448.—*DERMATOCARPON MINIATUM* (L.) Mann.—Abundant on limestone, in woods one-half mile north of Vernon, along the North Fork of Muscatatuck River, Jennings County.
- 7460.—*COLLEMA NIGRESCENS* (Hudson) D. C.—Sterile; on tree trunk; north of Vernon.
- 5493.—*LEPTOGIUM DACTYLINUM* Tuckerman.—On a sandstone ledge, Fern, Putnam County, 7 miles west of Greencastle.
- 7444.—*LEPTOGIUM CHLOROMELUM* (Swartz) Nylander. On oak trunk, north of Vernon.
- 6262.—Scraps of a juvenile *LEPTOGIUM*, probably *CHLOROMELUM*.—On limestone, under a ledge near Cataract Falls, Owen Park, Owen County.
- 7450.—*LEPTOGIUM JUNIPERINUM* Tuck.—On cedar bark, Schooner's Point, Crawford County; specimens very scanty. Spores $7-9 \times 15.5-24 \mu$.
- 7449.—*LEPTOGIUM PULCHELLUM* (Ach.) Nyl.—On a fallen tree, east of Vernon. In addition are two small specimens without data, from the DePauw Herbarium.
- 7458.—*PELTIGERA CANINA* (L.) Willd.—A scrap from Sword Moss Gorge, 14 miles west of Greencastle.
- 7436.—*PELTIGERA POLYDACTYLA* (Neck.) Hoffm.—Juvenile, mixed with *Cladonia mitrula* and *Physcia virella*. On mosses, over limestone, north of Vernon.
- 7438 and 7439.—*PELTIGERA PRAETEXTATA* (Sommerf.) Wainio.—On mossy limestone, north of Vernon.
- 5494.—*PELTIGERA PRAETEXTATA* (Sommerf.) Wainio.—Specimens scanty, on base of tree trunks; Fern, Putnam County.
- 1917.—*LECIDEA RUSSELLI* Tuck.—Specimens scanty and sterile; on limestone, Cedar Cliff, near Harrodsburg, Monroe County.
- 7454.—*CLADONIA CARIOSA* (Ach.) Sprengel.—On soil, near Martinsville, Morgan County.
- 7452 and 7453.—*CLADONIA CRISTATELLA* Tuck. and *CLADONIA CRISTATELLA OCHROCARPIA* Tuck.—On soil in oak-hickory grove, near Martinsville.
- 5497.—*CLADONIA FIMBRIATA* (L.) E. Fries var. *CONIOCRAEA* (Floerke) Wainio.—On decaying log on wooded slope, Fern, 7 miles west of Greencastle.
- 7440.—*CLADONIA FIMBRIATA* var. *SIMPLEX* (Weiss) Flotow.—North of Vernon.
- 7451.—*CLADONIA FIMBRIATA* var. *SIMPLEX* (Weiss) Flotow.—Pigeon River sand dune, Lagrange County.
- 7456.—*CLADONIA FIMBRIATA CONIOCRAEA* and *CLADONIA FIMBRIATA SIMPLEX*.—On soil, The Shades, Montgomery County.
- CLADONIA FURCATA* (Hudson) Schrader.—From herbarium of DePauw University; without data.
- 5576.—*CLADONIA MITRULA* Tuck.—On soil in woods, one-half mile south of Lake Cicott, Cass County.
- 7434, 7436, 7440, 7443, 7445.—*CLADONIA MITRULA* Tuck.—Evidently abundant in woods along North Fork of Muscatatuck, north of Vernon, on soil, mossy limestone, tree trunks, and decaying logs.
- 7455.—*CLADONIA MITRULA* Tuck.—On soil, The Shades, Montgomery County.
- 7456.—*CLADONIA PYXIDATA* (L.) Hoffm.—A few podetia, mixed in with *CLADONIA FIMBRIATA CONIOCRAEA* and *CLADONIA FIMBRIATA SIMPLEX*.
- 7459.—*PARMELIA CAPERATA* (L.) Ach.—On a fallen tree, east of Vernon. No. 7447, an isidiose scrap, seems to belong here.
- 7462.—*PARMELIA QUERCINA* (Willd.) Wainio.—On a dead tree, east of Vernon.
- 7461.—*PHYSICIA SETOSA* (Ach.) Nyl.—On a tree trunk, east of Vernon.
- 7435, 7437, 7442.—*PHYSICIA VIRELLA* (Ach.) Flagey.—Running over mosses on limestone, north of Vernon; mixed with other lichens and apparently common. Greenish yellow soredia are abundant along the margins; medulla white; no chemical reactions.

The Characteristic Plant Microfossils of the Pittsburgh and Pomeroy Coals of Ohio*

R. M. Kosanke

Introduction

A knowledge of the fossil flora of successive geological periods provides a basis for determining the relative position of geological strata much in the same manner as does the fossil fauna. Plant microfossils of the coal measure plants, preserved in coal, offer a clue to the plant communities of the Carboniferous period in the same manner as do pollen grains and spores to the paleoecologist working with Quaternary peat deposits. Variations in these plant communities are seen in the change of spore types throughout the coal bearing rocks which have been investigated. These variations may possibly be correlated with different types of coal.

Coal measure spores may be studied from coal maceration residues and filtrates, thin sections of coal, nitrocellulose peels, and thin sections of coal balls which contain fructifications. The maceration of coal has proven to be the best method in recent years for morphological and statistical studies. Through the study of petrifications, however, the natural affinities of spores may be established. The maceration method has been employed in this study.

Raistrick (1935) stated that "Correlation by microspores can be carried to considerable distances in the constant seams, but beyond local comparisons it soon becomes very problematic among the inconstant seams." Papers by Raistrick in 1937 and 1938 clearly indicate the value that microspores may have in correlation work.

The purpose of this investigation has been (1) to determine the characteristic plant microfossils of the Pittsburgh and Pomeroy coal seams of Ohio; (2) to describe such new species as are abundantly represented and lastly, (3) to determine if the Pittsburgh coal seam can be distinguished from the Pomeroy coal seam on the basis of plant microfossil content.

History of Ohio Coal Spore Studies

R. Thiessen and associates published a series of papers (1920-1932) in an attempt to correlate the various coal beds of Pennsylvania, Ohio, West Virginia, and Kentucky. The coal was studied microscopically, i.e., by means of thin sections of coal. Various spore types were used as index fossils. Their conclusions published in 1924 in a paper entitled "Correlation of Coal Beds of the Allegheny formation of western Pennsylvania, and eastern Ohio." "As

* This investigation was carried out in the Department of Botany, University of Cincinnati, Cincinnati, Ohio.

a result of this investigation it has been found possible to correlate each bed by means of spores and other structures found therein."

The stratigraphers, however, have been slow to accept the work of Thiessen and his associates. One reason for this may be that the spores were identified only from thin sections of coal. Few spores can be consistently identified by this method. However, Thiessen's work is important, because it was the first attempt in this country to study the spores of various coal beds systematically. Binary names were not given to the various spores described, but only type names.

Taxonomic Considerations

R. Potonié (1931) grouped all such spores under the name "*Sporites*" of H. Potonié (1893).

Ibrahim (1933) proposed a new artificial system for classifying spores. He divided all spores into three groups: (1) Trilites, spores with a tetrad dehiscence scar; (2) Aletes, spores without a dehiscence scar; (3) Monoletes, spores with evenly marked dehiscence scar. Although all spores were given binary names in the accepted fashion, much confusion has resulted from Ibrahim's paper. Unfortunately he used a name "Trilites" for one of his three groups, a name previously used in a generic sense by Bennie and Kidston (1886). Furthermore, the generic names applied to the spores are so similar that confusion has resulted, as can readily be seen by the following: Group "Trilites," *Punctati-sporites* is used for spores which possess a tetrad dehiscence scar and a sandy spore coat; Group "Aletes," *Punctata-sporites* is used for spores which have no dehiscence scar and a sandy spore coat; Group "Monoletes," *Punctato-sporites* is used for spores which have an evenly marked dehiscence scar and a sandy spore coat. Thus it is apparent that his terminology tells very little more than when all spores were grouped under the name "*Sporites*" of H. Potonié.

In the same year Raistrick and Simpson (1933) using the coal maceration method, fundamentally the same process as originally used by Schulze, were able to extract a large number of spores which they described, illustrated, and classified into six groups. Their groups were given letter symbols A-F.

Berry (1937) described fourteen species, some of which had been described previously but not named. He created the genus *Denso-sporites*.

Wilson and Coe (1940), in describing some microspores from Iowa, created four genera composed of twelve species some of which had been previously described but not named.

Schopf, Wilson, and Bental* realizing the confusion which exists at the present in the taxonomic treatment of microfossils have established the best classification of the known forms to date. Their analysis is followed in this paper.

* Unpublished manuscript.

Geology of the Pennsylvanian System in Ohio

The uniform and orderly arrangement of the Ohio rocks of the Pennsylvanian system were, for the most part, laid down under quiet water conditions. They were deposited in the Appalachian geosyncline far from the source of the sediments. Because of this the whole system in Ohio is marked by an abundance of finer silts, such as clays, shales, and by marine and fresh water limestones. The entire system contains less coal and sandstone but more clay,

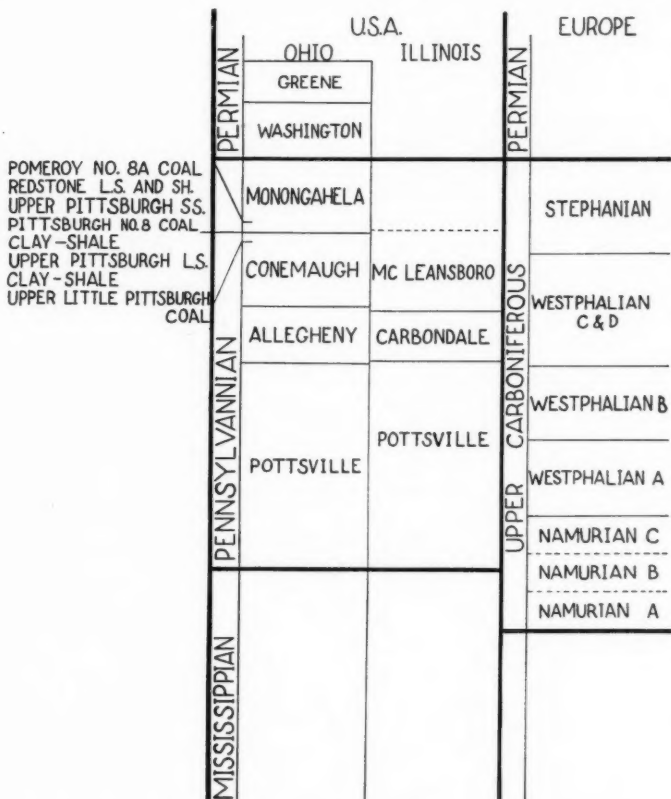


PLATE 1. A correlation chart showing the relationships of the Carboniferous divisions of Ohio, Illinois and Europe. The Pittsburgh No. 8 coal is shown as the basal member of the Monongahela series in Ohio. This is overlain by the Upper Pittsburgh sandstone generally, which in turn is overlain by the Redstone limestone and shale. The Pomeroy No. 8a coal (Redstone) is above the latter. (Stout 1930).

shale and limestone than are found in Pennsylvania, West Virginia, Kentucky, and Tennessee. Also the coals in Ohio are spaced very close together in the column in contrast to that found in western Kentucky, Illinois, and Iowa. Therefore the Pennsylvanian system in Ohio is characterized by fine grained sediments, the uniformity of deposition, and by their continuity over large areas (Stout, 1931).

Plate 1 is a correlation chart of the Pennsylvanian system of Ohio, Illinois, and western Europe. It is seen from this chart that the Monongahela formation is above the McLeansboro formation of Illinois and correlates with the Upper Stephanian of Europe. The Upper McLeansboro of Illinois might correlate with the Upper Little Pittsburgh coal of Ohio which is the top coal bed of the Conemaugh.

The Pittsburgh coal is known locally as the number eight coal and is the basal formation of the Monongahela series. The Pomeroy coal is known locally as the eight "a" coal and is also called the Redstone coal. The Pittsburgh coal is one of the most important coal beds of Ohio. Plate 2 shows the known localities of the Pittsburgh coal. The line of deposits crosses the state in a southwesterly direction from Jefferson County on the north to Lawrence County on the south, which is a distance of at least 170 miles. The maximum width of the area is about 50 miles; the minimum is about 25 miles.

"The Pomeroy (eight "a" or Redstone) coal bed was regarded as the Pittsburgh until 1907 when Condit showed that it lies above the Pittsburgh and on the horizon of the Redstone" (Brownocker and Dean, 1930). As shown in Plate 2, it is found primarily in Meigs, Gallia, and Lawrence Counties. It is best developed in Salisbury Township, Meigs County. This area is known locally as the Pomeroy field.

In *Analyses of Coals* by Brownocker and Dean, the ultimate analyses of the Pittsburgh and Pomeroy coals have been recorded for various mines throughout Ohio; an average of their figures show the following:

PITTSBURGH COAL

	From	To
Carbon	62.00%	77.85%
Hydrogen	4.81	6.00
Oxygen	6.01	18.00
Nitrogen	1.00	1.25
Sulphur	1.00	5.40
Ash	7.95	11.00

POMEROY COAL

	From	To
Carbon	62.00%	71.00%
Hydrogen	4.00	5.00
Oxygen	5.28	10.79
Nitrogen	1.19	1.23
Sulphur	1.42	5.00
Ash	9.38	20.00



PLATE 2. A section of south-eastern Ohio showing the distribution of the Pittsburgh and Pomeroy coal fields.

Thus it appears that the Pittsburgh coal contains more carbon and oxygen than does the Pomeroy coal. A higher carbon content is often correlated with a smaller amount of recognizable plant remains. The present study does not always bear out this contention, for certain Pittsburgh coal collections have shown the reverse to be the case.

Collections of Pittsburgh and Pomeroy Coal Seams

Ten collections were made throughout these two seams, two of which were made at mines which are definitely known to be Pittsburgh coal, and two which are definitely known to be Pomeroy coal. The remaining six collections have been associated with one or the other of these two seams. The collection areas are shown on Plate 2. The exact location and numbering system of the slides prepared in connection with this work are as follows:

Collection No. 1. Powhatan Coal Mining Company, Powhatan Point, Belmont County, Ohio. Slide numbers are 1 to 499. A generalized section of this collection is shown on plate 2.

Collection No. 2. Hanna Strip Mine, 3 miles N.W. of Georgetown, Harrison County, Ohio. Slide numbers are 500 to 999. The characteristic "roof coal" was present as shown on plate 2. The main seam was four feet six inches thick and ten core samples were taken at this point.

Collection No. 3. Taken along the banks of Shade River near Shade, Athens County, Ohio. The seam is slightly over one foot thick and the slide numbers are 1000 to 1250.

Collection No. 4. Same locality as collection three and the slide numbers are 1251 to 1499.

Collection No. 5. North Hill (Athens), Athens County, Ohio. A road cut exposure with intermittent seams of coal. The slide numbers are 1500 to 1999.

Collection No. 6. A road cut exposure on Highway 33, $\frac{1}{8}$ mile north of Burlingham, Athens County, Ohio. The slide numbers are 2000 to 2400.

Collection No. 7. A road cut on Highway 33, 1.7 miles south of the Athens County line in Meigs County, Ohio. The slide numbers are 2401 to 2999.

Collection No. 8. Princess Pat Mine on Highway 33, 3.5 miles north of Pomeroy in Salisbury Township, Meigs County, Ohio. A generalized section is shown on plate 2. Nine core samples were taken and the slide numbers are 3000 to 6051.

Collection No. 9. Same locality as collection eight. The slide numbers are 7000 to 8000.

Collection No. 10. $\frac{1}{8}$ mile north of Fossil Creek near Shade, Athens County, Ohio.

Methods

The method used to prepare the coal for microscopic study is a variation of methods described by McCabe (1931), Raistrick (1933), and Wilson (1940). Small fragments of coal were placed in a flask and covered with Schulze's solution for 48 to 100 hours depending upon the type of coal being treated. The solution was then diluted with distilled water and after decanting and washing several times the material was ready for the next process. The coal was then covered with ammonium hydroxide or potassium hydroxide, depending upon the nature of the coal. After 8 to 48 hours the solution was diluted with distilled water, after which, through decanting and washing, the

solution reached a pH of approximately 7. This was followed by screening of part of the mixture through a 1 mm. wire mesh screen and the remainder through a smaller wire mesh screen. This type of screening allows the smaller spores to be segregated and studied without being covered by the larger ones.

Glycerin jelly mounts are not permanent and as spores can not be mounted in balsam successfully, experiments with new mounting media were made. It was found that spores in glycerin jelly spread thinly over glass slides and the mixture evaporated, adhere well to the slide. Then a drop of balsam may be placed over the glycerin mount and a coverslip added. The material mounted in this glycerin-balsam manner has kept perfectly for over two years. It is hoped that this method of mounting will preserve the material longer than the standard glycerin mount. Another mounting medium, diaphane, is being used successfully (Schopf, 1938).

Description of Microspores from Pittsburgh and Pomeroy Coal Seams in Ohio

The following microspores belong to new species:

Genus *LAEVIGATO-SPORITES* (Ibrahim, 1933) emend. S.W.B.*

Laevigato-sporites Thiessenii sp. nov.

Plate 3; Figs. 1, 1a, & 1b

Symmetry: spores bilateral and monolete.

Shape: elongate oval in the plane of longitudinal symmetry, round or oval in transverse plane. When compressed the spores tend to elongate still further or become spherical.

Size: various forms range from 14 to 24 microns in length and slightly less than half their length in diameter.

Ornamentation: loosely to sharply verrucose forming intermittent ridges and valleys.

Haptotypic structures: a simple monolete linear suture, generally without lips, which often extends more than half the length of the spore. The suture often becomes inconspicuous if it coincides with several ridges.

Spore coat: 1 to 2 microns in thickness; ridges blue-green in color, valleys yellow.

Affinities: this species is not known in connection with any fructification. However, Fredda Reed (1938, p. 333) has figured spores from a Calamarian fructification which belong to the same genus. Some species of *Laevigato-sporites* are similar to spores obtained from a Filicinean type of fructification (Schopf, Wilson, and Bentall).*

Type locality: Hanna Strip Mine, Harrison Co., Ohio.

* Unpublished manuscript.

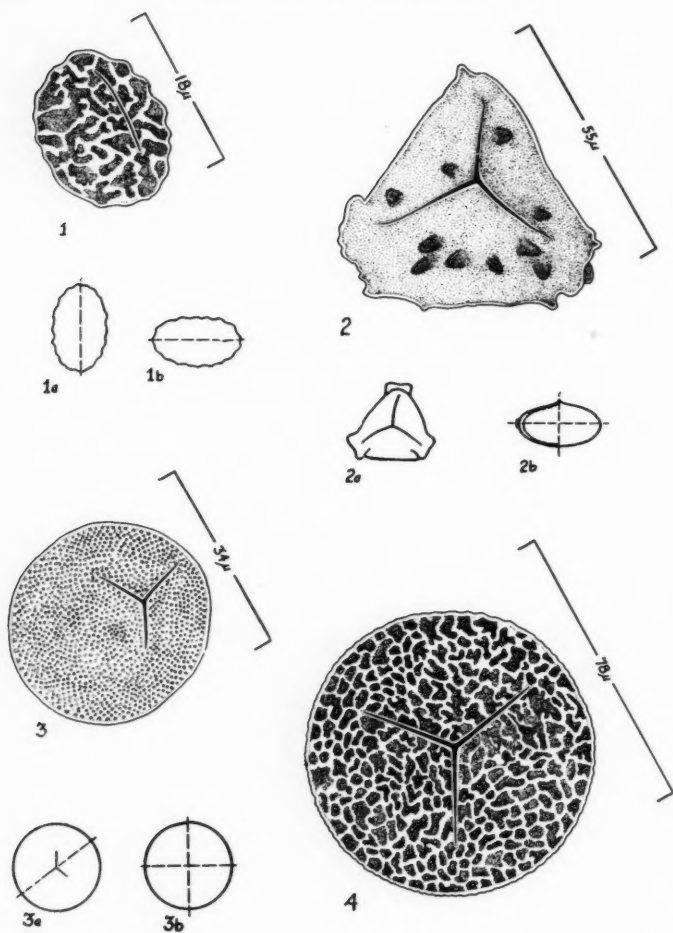


PLATE 3. Fig. 1. *Laevigato-sporites Thiessenii*, photo tracing; 1a, equatorial (transverse) plan; 1b, longitudinal plan corresponding with the longest axis. Fig. 2. *Triquirites spinosus* in axial view, photo tracing; 2a reconstruction after Schopf, Wilson and Benthall*; 2b, equatorial (transverse) plan — dashed line indicates spore cavity and shows the thickened spore coat at one of the radial angles. Fig. 3. *Punctati-sporites parvipunctatus*, photo tracing; 3a, equatorial (transverse) plan; 3b, axial plan. Fig. 4. *Punctati-sporites grandiverrucosus*, composite photo tracing.

* Unpublished manuscript.

Reinhardt Thiessen first observed this spore and called it the "Pittsburgh" spore (1923). A number of years later he called this same spore the "Pittsburgh microspore." He pictured it (1932, p. 21) and attempted to demonstrate a tetrasporic mark. This in reality a monolete suture with a crack at right angles. However, since Thiessen was the first to observe and illustrate this microfossil, I propose to call it *Laevigato-sporites Thiessenii*. This spore is not reported other than from the Pittsburgh coal seam as yet. The genotype slide is No. 551.

Genus PUNCTATI-SPORITES (Ibrahim, 1933) emend. S.W.B.*

***Punctati-sporites parvipunctatus* sp. nov.**

Plate 3; Figs. 3, 3a, & 3b

Symmetry: spores radial, trilete.

Shape: nearly spherical or occasionally irregularly spherical, rarely compressed.

Size: 32 to 38 microns in diameter.

Ornamentation: the surface is finely punctate and is further characterized by a yellowish color.

Haptotypic structures: each of the trilete suture rays are at least 9 to 10 microns in length; lips of the commissure usually distinct.

Spore coat: usually about 2 microns and rarely in excess of 3 microns.

Affinity: Kidston (1906) obtained from some *Crossotheca* fructifications, spores remarkably similar to those assigned to this genus, *Punctati-sporites*.

Type locality: Shade, Athens Co., Ohio.

The specific name *parvipunctatus* is proposed because it is the smallest spore known to this genus and the punctations are very fine. The genotype slide is No. 8026.

***Punctati-sporites grandiverrucosus* sp. nov.**

Plate 3; Fig. 4

Symmetry: spores radial, trilete.

Shape: spherical, occasionally splitting at the tetrad scar or suture.

Size : 73 to 92 microns in diameter.

Ornamentation: spores are very characteristically verrucosely sculptured.

Haptotypic structures: trilete sutures (each ray approximately $\frac{1}{3}$ the diameter of the spore) extend almost to the margin of the spore wall; lips thick and distinct.

* Unpublished manuscript.

Spore coat: 1 to 3 microns thick; external side irregular due to the verrucose sculpturing.

Affinity: same as previous species.

Type locality: Hanna Strip Mine, Harrison Co., Ohio.

Thiessen (1932) has a very good illustration of this spore (p. 21). He calls it the "Pittsburgh megaspore" based on a diameter distinctly under one hundred microns. Its interpretation as a megaspore is questionable and is not considered as such in this paper. The spore would seem to belong within the confines of the genus *Punctati-sporites*. The specific name *grandiverrucosus* is proposed because the spore coat is distinctly sculptured and the spore is the largest member of the genus *Punctati-sporites*. The genotype slide is No. 802.

Genus TRIQUITRITES Wilson & Coe 1940

Triquitrites spinosus sp. nov.

Plate 3; Figs. 2, 2a, & 2b

Symmetry: spores radial, trilete.

Shape: oval to elliptical in vertical plane; the horizontal plane is triangular in outline, corners rounded or truncate with a conspicuous thickening of the spore wall at this point.

Size: 45 to 55 microns in diameter.

Ornamentation: surface levigate and interspersed with spines.

Haptotypic structures: trilete rays extended nearly to the margin of the body cavity; lips prominent.

Spore coat: 1 to 2 microns thick except at the corners, which are much thicker; yellowish in color.

Affinity: unknown.

Type locality: Princess Pat Mine, Meigs Co., Ohio.

This spore is similar to *Triquitrites arculatus* Wilson and Coe except that it is distinctly spiny and slightly larger. Therefore the specific name *spinosus* is proposed for this microspore. The genotype slide is No. 8004.

In addition to the new species described, a number of previously known forms were present. The following list includes the new species and previously described forms which characterize the Pittsburgh coal in Ohio:

Laevigato-sporites Thiessenii sp. nov. is the most abundant microspore of the Pittsburgh coal and is not known from any other horizon.

Laevigato-sporites desmoinesensis (Wilson and Coe 1940) emend. S. W. & B.* is the next most abundant microspore. It has been reported from western Germany, West Virginia, Ohio, and Iowa.

* Unpublished manuscript.

Laevigato-sporites minimus (Wilson and Coe 1940) emend. S.W. & B* also has been reported from western Germany, England, West Virginia, Ohio, and Iowa.

Punctati-sporites grandiverrucosus sp. nov. occurs fairly abundant.

Punctati-sporites spinulistratus Loose 1932 reported from western Germany.

Calamospora hartungiana Schopf, Wilson, & Bental* reported from Illinois and now also known in Ohio.

Raistrickia grovensis Schopf, Wilson, & Bental* reported from Ohio and Illinois. Occurs rarely.

Endosporites ornatus Wilson and Coe 1940 reported from western Europe, West Virginia, Ohio, and Iowa.

The following microspores are characteristic of the Pomeroy coal seam in Ohio:

Endosporites ornatus Wilson and Coe 1940 is one of the most abundant and diagnostic microspores of the Pomeroy coal seam.

Laevigato-sporites desmoinesensis (Wilson and Coe 1940) emend. S.W. & B* is an abundant microspore of the Pomeroy coal seam.

Laevigato-sporites minimus (Wilson and Coe 1940) emend. S.W. & B* is equally abundant as the preceding species.

Calamospora hartungiana Schopf, Wilson, and Bental* is one of the more abundant spores of the seam.

Punctati-sporites parvipunctatus sp. nov. occurs regularly and is easily recognized.

Triquitrites spinosus sp. nov. occurs regularly.

Pityosporites (?) Seward 1914. Occurrence is extremely rare. This genus has been described by Virkki occurring in the Gondwana deposits and by Florin as occurring in the Stephanian of France. Further, the Stephanian of France correlates with the position of the Monongahela series (Plate 1) of Ohio.

Discussion

From the material examined in this study, certain microspores apparently have a limited vertical range in which they occur abundantly. Furthermore, each possesses features which enables certain identification. Thus it would appear that they are good index fossils which may be used in correlation. *Laevigato-sporites Thiesenii* sp. nov. and *Punctati-sporites grandiverrucosus* sp. nov. are valid indices of the Pittsburgh coal in Ohio. Approximately 75 per cent of all the spores extracted from the Pittsburgh coal are *Laevigato-sporites Thiesenii* sp. nov. *Punctati-sporites grandiverrucosus* sp. nov. occurs commonly and is easily recognized.

* Unpublished manuscript.

The Pomeroy coal is distinguished from the Pittsburgh coal by an abundance of *Endosporites ornatus* Wilson and Coe 1940, which occurs rarely in the Pittsburgh coal, and the presence of *Triquitrites spinosus* sp. nov. and *Punctati-sporites parvipunctatus* sp. nov. which have not been observed in the Pittsburgh coal. Also a negative fact is that *Laevigato-sporites Thiesseii* sp. nov. and *Punctati-sporites grandiverrucosus* sp. nov. have not been observed in the Pomeroy coal.

Summary

1. The characteristic plant microfossils of the Pittsburgh and Pomeroy coals have been determined.
2. Four new species of microspores have been described, named, and illustrated. They are: *Laevigato-sporites Thiesseii* sp. nov., *Punctati-sporites parvipunctatus* sp. nov., *P. grandiverrucosus* sp. nov., and *Triquitrites spinosus* sp. nov.
3. The Pittsburgh coal may be distinguished from the Pomeroy coal in Ohio on a basis of microfossil content.

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Notes on the Genus *Tempskya*

Henry N. Andrews

Petrified fern stems belonging to the genus *Tempskya* are now known from numerous Cretaceous localities throughout Europe and the United States. They have been reported from England, Germany, the Ural Mountains, Montana, Wyoming, Idaho, Utah, Oregon and Maryland. A few years ago Read and Brown (1937) and later Read (1939) presented summaries of our knowledge of the genus and described four American species, two of these being new. These were timely and well executed contributions and fortunately served to stimulate interest in these bizarre and problematical ferns.

It is the purpose of this note to record certain interesting facts relative to the distribution as well as probable habit and affinities of *Tempskya* as it will be some time before an exhaustive study of the recently acquired material in my own collection is completed, and much more collecting is also to be desired.

During the past few years I have made a number of short trips in the vicinity of the former town of Cumberland, located 16 miles south of Kemmerer, Wyoming, chiefly to obtain fossil plants from the Frontier formation (Upper Cretaceous). The conspicuous elements of this flora are *Anemia Fremonti* Knowlton and *A. Fremontii* forma *fertilis* Andrews, the latter name being used to designate the dissociated fertile fronds (Andrews and Pearsall, 1941). The material on which the form is based exists in an excellent state of preservation and there is no doubt as to the validity of the family and generic designations. The possible bearing that these fossils have relative to the *Tempskya* stems will be revealed presently.

In their report on *Tempskya* Read and Brown record specimens of *T. minor* from the Aspen formation in the eastern and northeastern corner of the Afton quadrangle, Lincoln county, as well as from the terrace gravel near Fossil, Wyoming. In view of the very durable nature of these petrified stems it is quite likely that the latter represent wash material from the Aspen shales located some twenty-one miles east of Fossil. A specimen that I obtained from there a few years ago evinced long transportation. In view of this we prospected the Aspen formation which outcrops along a north-south line shortly east of Kemmerer for some few miles in July, 1941, with very favorable results. Collections were made at two localities, one approximately nine miles northeast and the other ten miles southeast of Kemmerer, the latter yielding the better material. In all cases the trunk fragments had weathered out of the formation and were partially covered by soil and sagebrush but most are specimens exhibiting sharp angular breaks indicating their nearby origin in the Aspen formation.

Seventy specimens were collected in all consisting of trunks (false stems)

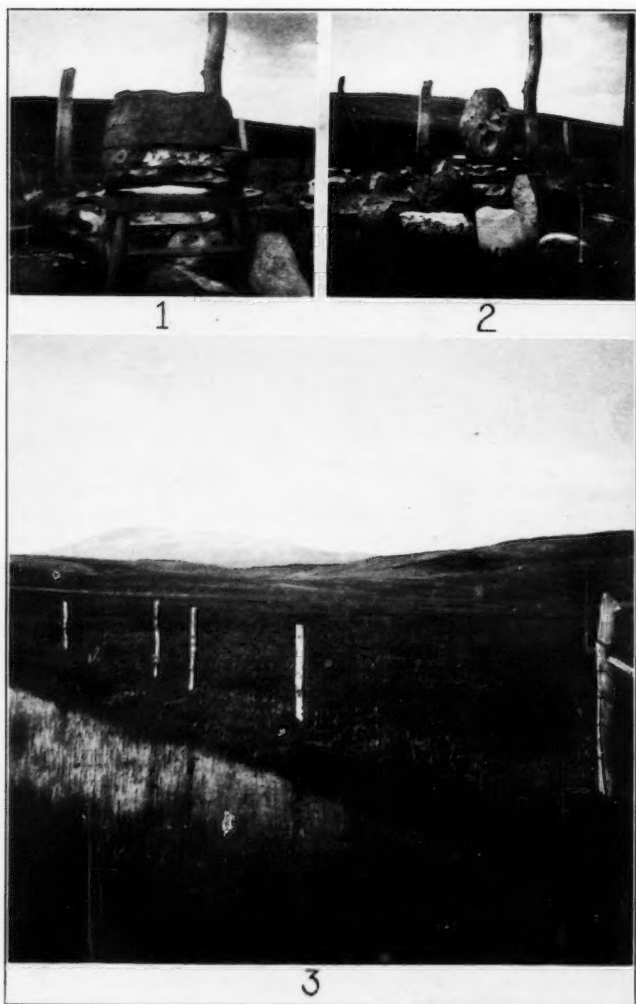


PLATE 1: Figs. 1 and 2. *Tempskya* specimens in the collection of Mr. C. H. Thomas, Wayan, Idaho. Dimensions given in text. Fig. 3. Foreground includes part of the former Thomas ranch near Wayan. Many specimens were collected from a stream bed running through the center of the photograph.

up to six inches long and varying from one and one-half to seven and one-half inches in diameter. Many are distinctly oval in cross section, others circular or nearly so. In view of the relative abundance of specimens in this region and their recorded occurrence farther north in Lincoln county it is probable that further search will disclose many other localities along the narrow, extended outcrop.

Returning now to the Frontier formation which immediately overlies the Aspen it may be noted that the fronds of *Anemia Fremonti* were collected only a few miles southwest of the *Tempskya* deposits noted above. This association does not, of course, offer anything approaching final proof of the schizaeaceous affinities of *Tempskya* but it is especially suggestive in view of the fact that Seward (1924) reported schizaeaceous sporangia annuli of the *Anemia* type mingled among the leaf bases of *T. Knowltoni* (from Montana).

Tempskya was certainly abundant in the Wyoming region in Cretaceous times and *Anemia Fremonti* is one of the dominant elements of the Frontier flora. Furthermore the abundance of these leaf remains brings up the question of the general habit of the plant that bore them. The living species of *Anemia* are low growing, favoring limestone sink holes and such places, neither an ideal habit or habitat for their preservation as fossils. Moreover, sterile fronds referred to *Anemia* have been reported from numerous Cretaceous and Eocene localities in the Rocky Mountain states and because of the rather distinctive features of the sterile as well as the fertile pinnae of this genus there is good reason to believe that the identifications are correct in many cases. If these fronds were borne on trunks of some appreciable height such as *Tempskya* it would be much easier to account for their occurrence as fossils. Much remains to be learned of these possible affinities but the evidence cited here certainly points toward rather than away from the inclusion of *Tempskya* in the Schizaeaceae.

A final point that I should like to mention, and one that previous descriptions have not brought out, is the great size that *Tempskya* trunks attained.

Early in the summer of 1942 I spent a few days in the field in southeastern Idaho in company with Mr. W. A. Peters of Jerome, during which time we collected about one ton of fine specimens. These were obtained from two localities near Wayan (NE $\frac{1}{4}$ sec. 35, T. 5S., R. 43E and SW $\frac{1}{4}$ sec. 13, T. 5S., R. 43E, Lanes Creek Quadrangle) and from a third locality 25 miles west of Ammon (NW $\frac{1}{4}$ sec. 5, T. 2N, R. 41E, Hell Creek Quadrangle). In all cases the specimens were apparently weathering out of the Cretaceous Wayan formation.

The first of these localities occurs on the former ranch of Mr. C. H. Thomas about two miles south of Wayan. Specimens were found in abundance in the creek bed a few hundred feet north of the ranch house. Mr. Thomas' own collection includes scores of fine trunks; the largest of these, shown in Fig. 2, measures $39\frac{1}{2}$ inches in circumference and 16 inches long; another (Fig. 1) measures $39\frac{1}{2}$ inches in circumference although it is somewhat

shorter. We were fortunate in obtaining a specimen of similar proportions (No. 1446, Washington Univ. coll.) from this locality.

The second locality, located on the south slope of a prominent spur approximately $\frac{1}{2}$ mile south of the Sibbett ranch, near Wayan, yielded many specimens from a recently plowed field. They had been found here in such abundance at one time as to allow their use for ranch house foundation stone.

Perhaps the finest specimen that we obtained came from the Pipe Creek locality west of Ammon. Included in this collection is a series of 5 trunk fragments (Nos. 1449, 1450, 1451), four of which were found within a radius of 2 feet and the other two but a short distance away. Three fit together perfectly forming a trunk section 6 inches in diameter by 13 inches long. The other two are 4 and 9 inches, respectively, the latter tapering to a blunt point, apparently the top. If, as is very likely, all five are from the same plant its total length was more than 26 inches. A similar specimen in the collection of Mr. E. Manion of Firth, who served as our guide on this trip, measures 9 inches by $2\frac{1}{2}$ inches long. This specimen shows no diminution in diameter at either end and is certainly a fragment of a long trunk.

If we may assume that the larger trunk sections measuring 38 to 39 inches in circumference came from proportionally long plants then a maximum length of 5 to 6 feet is not at all improbable for *Tempskya* stems.

I should like to express my thanks to Messrs. W. A. Peters, W. A. Brox, C. H. Thomas and E. Manion, local collectors, whose generosity has made possible the acquisition of most of the specimens in our collection.

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Suggestions for Using Foraminifera in Zonal Paleontology*

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This report is a discussion of the distribution and development of the genera *Bulimina* and *Buliminella* through a sequence of California Late Tertiary outcrops. It is presented as an example of the use of smaller Foraminifera for the organization of strata into zones.

The section is located at Cañada de Aliso, Ventura County, California. Here, in 1932, under the control of a plane-table traverse, about 500 samples were collected through 17,000 feet of well-exposed marine strata. In 1934, a set of assemblage slides containing mounted specimens from this collection was taken to the Cushman Laboratory for Foraminiferal Research for direct comparison with type material.¹ Independent study of the named genera by Miss Frances L. Parker has materially aided the investigation.

Chart I depicts several details concerning the distribution of the bulimines in the collection. On the left is a graphic columnar section. The stratigraphic placement of a few collecting stations is on the right side of this columnar section. The opposite side depicts stratigraphic thickness in feet, measured from the base of the lowest Repetto sandstone, the datum plane of this report.

Across the top of the chart are listed the names of the species of *Bulimina* (Blm.) and *Buliminella* (Blla).² Beneath each are indicated range, stratigraphic placement, and relative abundance. Ranges are delineated by heavy vertical lines. Stratigraphic placement is determined by carrying any point on the graphs horizontally to the columnar section. Relative abundance is shown by the width of the short horizontal lines bisected by the range lines. Their width was determined by actual count of specimens from a given amount of concentrate, translating the results to logarithms, and directly scaling the final figures across the range lines. This use of logarithms dimin-

* This paper originally appeared in the Proceedings of the Sixth Pacific Science Congress (2:665-670) and is republished by permission of the editors, Doctors C. B. Lipman and Roy E. Clausen. Republication, unusual in this journal, is justified by the extensive and continued demand for Mr. Adams' paper on the part of both students and professional paleontologists, by its limited availability in the original Proceedings, and by the desirability of bringing it to the attention of other workers through the medium of a journal that places emphasis on contributions to biostratigraphy and paleobiology.—THE EDITORS.

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² References to these species are listed in the Bibliography accompanying this article.

ishes distortion, which would result if forty or fifty specimens were directly measured in the same proportion as one or two.

The sketches of the Foraminifera are based on tracings made from camera lucida drawings by Mrs. Margaret Hughes. These were drawn to the same scale, indicated graphically on the lower right-hand corner of the chart. The arrows show placement of the figured specimens.

The morphology and distribution of several species will be discussed in order to illustrate methods of handling the fossils.

Bulimina fossa Cushman and Parker (II) ranges from just beneath the datum for 1200 feet stratigraphically higher. It is a species characteristic of the Repetto formation in California, although not readily distinguished from similar forms in other horizons. The modern analogues are *Bulimina buchiana* of Brady (not d'Orbigny) and *Bulimina rostrata* Brady, which appear to favor cool, deep water.

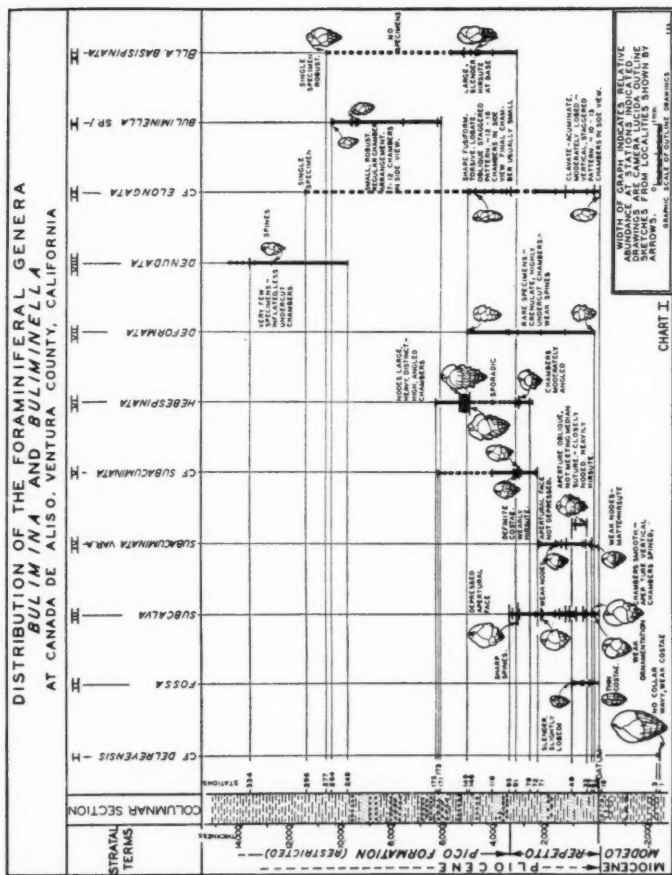
Bulimina subcalva Cushman and Stewart (III) is also a characteristic Repetto species, but of greater range. At Cañada de Aliso it extends from just beneath the datum for 3500 feet stratigraphically higher. The earlier chambers are variously ornamented with irregular spinose costae. The final chambers are typically smooth. A consistent character is the position of the aperture, situated vertically above the sutural junction of the three highest chambers within a well-depressed apertural face. Little morphological change in the development of the species was observed throughout its range.

Bulimina subacuminata, var. a (IV), *Bulimina* cf. *subacuminata* (V), and *Bulimina hebespinata* (VI) are alike in possessing apertures rising obliquely from slightly above the angled junction of the last three chambers. The aperture is sometimes carried across the upper end of the test, and is not within any well-defined depression. A certain degree of axial symmetry is common to all three variants.

Bulimina subacuminata, var. a (IV), is a hirsute to costate series, with indistinct, closely yet regularly set nodes. It ranges from 250 to 2300 feet stratigraphically above the datum. In a portion of its range appear several profusely ornamented specimens, covered with nodes and spinose processes.

Bulimina cf. *subacuminata* Cushman and Stewart (V) ranges from 2345 to 6340 feet stratigraphically above the datum. The determination is uncertain. It does not precisely resemble topotype material obtained from Humboldt County, northern California. It is definitely not the *Bulimina subacuminata* used by micropaleontologists for the Los Angeles Basin, which ranges higher, is more nodose, and lacks hirsute ornamentation. Our species is distinguished from the preceding variant by the presence of well-divided nodose costae.

Bulimina hebespinata R. E. and K. C. Stewart (VI) ranges from 2640 to 6385 feet above the datum. It is heavily ornamented, with high, undercut



chambers and pronounced nodes. It is divisible into a less ornate, smaller variety which ranges lower, and a highly ornate type which appears confined to a 300-foot shale body.

Bulimina deformata Cushman and Parker (VII) is a rare, sporadic species, roughly ranging between 190 and 5100 feet above the datum. It has angled, well-undercut, bluntly spined chambers. The aperture has a low collar, and the apertural face is strongly oblique to the vertical axis of the test.

Bulimina denudata Cushman and Parker (VIII) differs from *deformata*

(VII) in having more rounded, less undercut chambers. Spines are rare, but distinct. The species ranges sporadically from 9880 to 13,660 feet above the datum. It is very similar to *Bulimina etnea* Seguenza from the Pliocene of Italy.

Bulimina deformata and *Bulimina denudata* suggest more of a structural trend than an out-and-out species division. The trend is from crenulate, highly undercut chambers to inflated, less undercut chambers; from dull tests to lustrous tests; from nodose processes to sharp spines. Similar species living off the west coast of America are *Bulimina pulchella* d'Orbigny, with less inflated chambers than *denudata* and spines confined to denticulate processes near the margins, and *Bulimina pagoda* Cushman, with well-inflated chambers and large, hooked spines.

Bulimina cf. *elongata* d'Orbigny (IX) is a rare but persistent species ranging from just beneath the datum for 11,490 feet above. The forms grouped under this category also exhibit a structural trend; up to 2500 feet above the datum the specimens are clavate at the upper end, tapering toward the base; higher, they are fusiform and more lobed. The lower specimens show a vertically staggered chamber arrangement; the higher ones are obliquely staggered and the chambers smaller, more rounded. Ten to twelve chambers can be counted in side view for the lower mutation; twelve to sixteen chambers are the rule above this. In addition, the higher type has a torsive test and the final chamber is typically small, somewhat suggestive of the genus *Neobulimina*.

The foregoing information concerning the distribution of the genera *Bulimina* and *Buliminella* is next combined with a previous report on the genus *Bolivina*³ from the same collection.

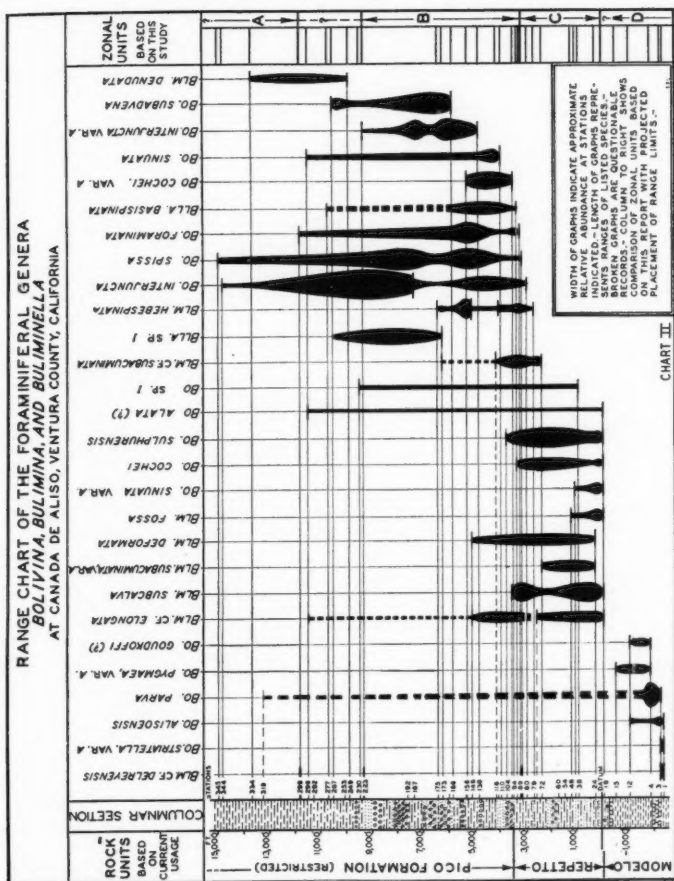
Chart II presents the results. The plan of this chart is much the same as that for the first; however, the range graphs are generalized as to relative abundance. No effort is made to depict the structural trends.

The numerous horizontal lines represent range limits of the individual species. The observer will note that these lines may be combined into three broad stratigraphic groups, which may be termed belts of demarcation.

The first is that beneath the datum place, where nine species appear for the first time. This is not an ideal zonal boundary, however, as the change is abrupt, with insufficient records of species crossing the division. A glance at the lithologic column confirms the impression that this is a facies break. It may be an unconformity.

The second belt of strata is delimited by numerous range lines. Their total mass throws emphasis upon a narrow segment of strata about 3200 feet stratigraphically above the datum. This sharp boundary is brought into focus by concentration of the data.

³ B. C. Adams. Distribution of Foraminifera of the Genus *Bolivina* in Cañada de Aliso, Ventura County, California. *Am. Jour. Sci.* **237**:500-511, 1939.



The third belt is vague. The bolivines and bulimines contribute little to this portion of the section. It is wide enough to be termed a belt of transition.

Between these belts of strata are placed letters to designate four provisional units defined by the present study.

Unit A roughly coincides with the shale member of the Upper Pico formation. It is to be regarded with suspicion as it lacks sufficient records.

Unit B is not only better defined, but it may be further divided, as between the upper range of *Bulimina hebespinata* and the lower limit of *Buliminella* sp. 1.

Unit C is featured by the restricted occurrence of five species.

Unit D is marked by four ranges and the only abundant records of *Bolivina parva*.

Scrutiny of these charts reveals several facts.

1. There is a close relationship between the fossils and the sediments. Thus, the belt of transition between provisional zones A and B falls between two mappable units. The higher consists of a massive shale sequence; the lower one carries alternating beds of sandstone, silt, and conglomerate. Here, as in other parts of the world, zonal boundaries may sometimes coincide with cartographic divisions.

However, this is a point in paleoecology and may not be reduced to lithologic terms. For example, the clearest zonal division in this report is that between units B and C, which are not readily separated by their lithology. Furthermore, the fauna in *Unit C* also occurs in a massive silt section in the Repetto Hills, Los Angeles, California. These sediments differ from the sandstone, silt, and conglomerate of Cañada de Aliso.

The succession suggests a vertical facies change. For example, *Unit D* indicates a past deep-water environment, or else a protected embayment permitting deposition of finely bedded clastics, such as siliceous shale. *Unit C* shows moderately deep-water marine conditions accompanied by disturbance induced either by diastrophism or other conditions causing change of sedimentation. *Units B* and *A* denote decreasing depth of the sea.

The vertical facies record is a local series of events attested by the sequence of deposits and contained fossils. It is applicable to this particular section. The *Units* defined by it are not of zonal significance for the reason the study must be expanded to other control sections and to other areas before the ranges of the species are known.

Nevertheless, a succession similar to that at Cañada de Aliso is found 600 miles to the north, in Humboldt County, California. There, the faunal sequence of *Units C* to *A* is roughly repeated. In other words, the past ecologic controls that govern the distribution of Foraminifera may themselves be of regional magnitude.

2. You will notice certain structural trends within several of the species. One example is the group of *Bulimina subacuminata* variants (IV, V, VI). Other species are relatively stable, such as *Bulimina subcalva* (III). Some forms are too short-ranged to show indications of any type of trend, such as *Bulimina fossa* (II). Still others suggest structural trend but are too rare for satisfactory analysis, such as *Bulimina deformata* (VII), and *Bulimina denudata* (VIII).

These structural trends are not always readily reduced to black and white. In spite of this, the obscurely defined mutations of the *Bulimina subacuminata* group are now being successfully used among other criteria for dividing the

California Pliocene by micropaleontologists. The structural trends may be vague with respect to outline and definition, but clear and crisp with respect to time value. The technique is one familiar to most students of graptolites and echinoids.

3. There are three types of occurrences. (a) Some species are relatively long-ranging, and are not restricted to any of the provisional zones. (b) Other species have their lowest stratigraphic record in one zone, but extend into the next higher. (c) A few species are restricted to a given zone.

These three types of distribution constitute the essential basis for the establishment of zones. It is this staggered distribution of species that makes true zones independent of lithologic units.

4. Experience in collecting and laboratory study demonstrates that our ability to determine range limits of species is affected by two variables: the spacing of collection, and discrimination of species. The first of these is mechanical; thus, were one sample not collected, the range of *Buliminella basispinata* (XI) would be lowered by 4300 feet on the chart. On the other hand, still closer collection might demonstrate whether this was indeed a definite range or an unexplained occurrence.

The second variable reflects an individual's philosophy. Thus, another worker may decide that the species *denudata* and *deformata* are not to be divided on a list. In this way but one range would appear through a considerable thickness of rock.

Some useful points to emphasize in classifying the species of *Bulimina* and *Buliminella* are: nature of the wall material and its perforation, size and shape of test, pattern of the chambers, and character of the aperture. Other details, such as surface ornamentation, are worthy of sharp scrutiny to detect morphologic trends within the species.

Briefly stated, those morphologic details which are more closely related to the growth and development of the animal need relatively stronger emphasis for the discrimination of species.

These and other variables must be surmounted in using Foraminifera for defining zones. Methods of attack in this direction were established some time ago by such stratigraphers as Oppel, Spath, Diener, Hyatt, Smith, and numerous others handling ammonites. It is the technique employed by workers with other types of fossils, such as Lapworth with the graptolites, or Henry Shaler Williams with trilobites and brachiopods. Recently, R. M. Kleinpell has applied the same principles to a classification of the California Miocene by means of the smaller Foraminifera.

The following steps are helpful in using the smaller Foraminifera for stratigraphic classification.

1. Use of closely collected control sections in each province. Ideal sections for this purpose would be located well away from the edge of the basin of

deposition, in order to avoid facies extremes; they would lack structural flaws such as faults or unconformities; lastly, they would carry well-preserved fossils throughout their extent.

2. Discrimination of species based not only on morphology, but also on their vertical development and lateral distribution.

3. Erection of zones. This can be accomplished by first forming provisional divisions and then testing and improving these by study and comparison with numerous sections throughout the area of investigation.

If there is time for the added research, an alternative method is to study the various sections fully before making any divisions at all. This affords a broad perspective and improves the possibilities for overcoming the problem of facies. If such a study is pursued across a large area, the opportunity to erect valid zones is greatly increased.

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THE TEXAS COMPANY,
LOS ANGELES, CALIFORNIA.

Records and Descriptions of North American Crane-Flies (Diptera)¹

Part III. Tipuloidea of the Upper Gunnison Valley, Colorado

Charles P. Alexander

In the present report are discussed the partial results of extensive collections of Tipuloidea that were taken in the vicinity of Gothic, Gunnison Co., Colorado, in 1934, chiefly by Mrs. Alexander and the writer. It is hoped that we will be able to make a detailed survey of the crane-flies of the entire Rocky Mountain system and the western United States and Canada, a study that will require a vast amount of work during the next several years. In 1941, in Wyoming and Colorado, very extensive series of these flies were taken that will be discussed in future parts under this general title.

General Account

The so-called "Gothic Area," site of the Rocky Mountain Biological Laboratory, lies in the Gunnison National Forest, Gunnison Co., in west-central Colorado. One of the sources of the Gunnison River, East River, flows through the Gothic Area and much of the collecting done at Gothic was along or near this beautiful mountain stream. East River eventually flows into the Gunnison, which in turn flows via the Grand River into the Colorado and into the Gulf of California. All collecting in the area was thus to the west of the Continental Divide.

The facilities of the Rocky Mountain Biological Laboratory (Dr. John C. Johnson, Director, Crested Butte, Colorado) were made available to us in 1934 and we are greatly indebted to various members of the staff and student body of 1934 for much co-operation in our work. Our thanks are extended to Dr. and Mrs. Johnson, Dr. A. O. Weese, Dr. and Mrs. George W. Hunter III, Dr. and Mrs. B. D. Barclay, Dr. Mary F. Howe (Mrs. M. H. Schott), Dr. J. Teague Self, and, from the student body, Mr. John D. Hallahan. The last-named was keenly interested in insect collecting and we are very greatly

¹ The preceding part under this general title was published in the *American Midland Naturalist* **26**: 281-319; 1941.

References in the text refer to the bibliography at the conclusion of the general account.

In all cases where no collector is given, the specimens were secured by the author. M. M. Alexander—Mrs. Charles P. Alexander.

indebted to him for many fine specimens. In 1935, our former student, Dr. Inez W. Williams, was an advanced research student at the Laboratory and collected further extensive series of Tipuloidea, these including the only specimen of the primitive family of Tanyderidae ever taken in the area.

The brief account of Gothic prepared for the annual announcement of the Laboratory is so excellent that I am taking the liberty of quoting part of it.

The Gothic Area comprises about a half million acres of virgin territory, almost uninhabited. There are numerous high mountains, rivers and streams, lakes, bogs, swamps, mountain and alpine meadows and regions of perpetual snow. The great range in elevation (8,000 to 14,000 feet) makes for great diversity in fauna and flora and offers examples of many different ecological communities.

In 1930 the U. S. Forest Service set aside the "Gothic Natural Area," in the Gunnison National Forest, a permanent research tract of about 905 acres, not far from the laboratory. Of this area some 500 acres is a virgin spruce-fir forest, while the other 400 acres is composed of alpine meadows, marshland and open grassy parks.

The remarkably rich environment of the Rocky Mountain Biological Laboratory, in conjunction with a splendid staff, makes this area an ideal one for the study of the insect fauna in many groups, still almost unworked.

Mrs. Alexander and I arrived at Gothic on July 1st, 1934 and remained until August 8th. The general altitude of the laboratory and immediate vicinity is 9,500 feet; collections were made up the sides of Gothic Mountain to over 10,000 feet; Mount Avery to above 10,000 feet; along Copper Creek to above Judd Falls; up the Gothic Valley along East River to Emerald Lake, 10,500 feet; and in the Biological Forest, or "Gothic Natural Area," at about 10,000 feet.

One restricted area across East River from our cottage (Bellevue Cottage) was made the base for special study. This occupies a swampy area with considerable growth of Engelmann's Spruce, *Picea engelmannii* (Parry) Engelmann, and Alpine Fir, *Abies lasiocarpa* (Hooker) Nuttall, together with other characteristic plants of this association, including *Equisetum*, *Saxifraga arguta* Don., *Swertia palustris* A. Nels., *Gentiana elegans* A. Nels., and *Lonicera involucrata* Banks.

The stations in the Upper Gunnison Valley where collections were made lie in the upper Canadian life zone and in the lowest Hudsonian. The slopes of the mountains and the vicinity of Emerald Lake are definitely higher Hudsonian. No collections were made outside of these two zones. Following the classification of the United States into the physical divisions adopted by Fenneman and co-workers (Fenneman, 1931), the Gothic Area falls in the Southern Rocky Mountain Province of the Rocky Mountain System.

In addition to the species recorded at this time, there still remain a considerable number of additional forms that I have not been able to identify satisfactorily to the present moment. Most of these belong to the genus *Tipula*, including a vast range of species in western North America.

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Systematic Account

TANYDERIDAE

Protanyderus vipio (Osten Sacken, 1877).—Gothic, 9,500 ft., July 6, 1935 (Inez W. Williams), swept from vegetation along the East River.

PTYCHOPTERIDAE

Ptychoptera pendula Alexander, 1937.—Not uncommon in the Gothic Area, especially so along a small, clear mountain stream, 10,100 ft., on road to Emerald Lake, July 12, 1934.

TRICHO CERIDAE

Diazosma subsinuata (Alexander, 1916).—Gothic, 10,000 ft., July 5, 1934 (Hallahan); 9,500 ft., July 23, 1934 (M. M. A.).

TIPULIDAE

TIPULINAE

Tipula (*Bellardina*) *gothicana* sp. nov. — General coloration of mesonotum buffy yellow, the praescutum with four brown stripes that are narrowly bordered by darker brown; femora brownish yellow, the tips narrowly blackened, preceded by a very vague, obscure yellow, subterminal ring; wings with the ground color grayish brown, sparsely variegated by darker brown and cream-colored areas; abdominal tergites reddish brown, narrowly darkened on sides; male hypopygium with the median region of tergite produced into a conspicuous depressed-flattened lobe, its caudal margin with an oval notch.

♂. Length, about 17-19 mm.; wing, 17-20 mm.; antenna, about 3.3-3.5 mm.

♀. Length, about 18-19 mm.; wing, 22 mm.

Frontal prolongation of head relatively long, yellowish brown on sides, darker above; nasus long and slender; palpi brown. Antennae (male) of moderate length; scape brownish yellow, pedicel clear light yellow, flagellum

pale brown, the outer segments slightly more darkened; flagellar segments only weakly incised, with very long conspicuous verticils. Head dark brown, the front and orbits more brownish gray.

Pronotum brown, paler laterally. Mesonotal praescutum with the ground color buffy yellow, with four brown stripes that are narrowly and somewhat insensibly bordered with darker brown; intermediate stripes confluent on cephalic third or less, distinctly separated behind, reaching the suture; humeral and antero-lateral portions of praescutum darkened; scutum buffy gray, each lobe with two conspicuous brown areas, the more mesal ones almost touching one another on the median line; scutellum darkened basally, broadly more yellow behind, parascutella dark; mediotergite yellow, the cephalic two-thirds gray pruinose. Pleura and pleurotergite weakly darkened, more or less variegated with paler and darker areas, the latter including the ventral sternopleurite and meron, together with the pleurotergite above the root of halteres. Halteres with stem brownish yellow, knob infuscated, its apex yellow. Legs with coxae grayish brown, the tips pale, the posterior pair somewhat more intensely darkened; trochanters yellow; femora brownish yellow, the tips narrowly blackened, preceded by a very vague, obscure yellow, subterminal ring, the amount of black subequal on all femora; tibiae and basitarsi obscure yellow, the tips dark brown; remainder of tarsi passing into black; tibial spur

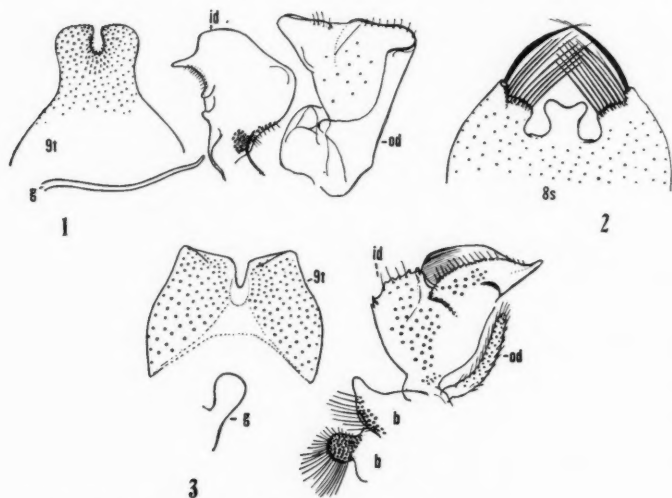


Fig. 1. *Tipula (Bellardina) gothicana* sp. n.; male hypopygium.

Figs. 2, 3. *Tipula (Lunatipula) barbata* Doane; male hypopygium.

(Symbols: b, basistyle; g, gonapophysis; id, inner dististyle; od, outer dististyle; s, sternite; t, tergite.)

formula 1-1-2; claw (male) toothed. Wings with the ground color extensively grayish brown, restrictedly variegated with darker brown and cream-colored areas, the darker markings, besides the stigma, including a very small spot at origin of *Rs*, two dark areas in outer half of cell *M* and another at near one-third the length of cell *Cu*; creamy areas in radial field beyond the stigma restricted in amount; distal fourth of cell *R*₅ brightened; other pale marginal spots in medial and cubital fields relatively restricted; veins brown. Numerous macrotrichia on outer radial veins, becoming more sparse on outer medial veins. Venation: *Rs* elongate, more than one and one-half times *m-cu*; cell *R*₃ constricted at midlength; cell 1st *M*₂ short.

Abdominal tergites reddish brown, narrowly darkened on sides; sternites yellow to obscure yellow; outer segments, including hypopygium, more infuscated. Male hypopygium (Fig. 1) relatively large and conspicuous; tergite fused with sternite. Ninth tergite, 9*t*, with median portion produced caudad into a conspicuous depressed-flattened blade, the posterior margin with a deep but narrow oval notch that is widest at midlength; lateral lobes broadly truncate; tergal blade with numerous setae of moderate length, those adjoining the notch shorter and more spinous. Mesal face of basistyle with a group of long conspicuous setae. Outer dististyle, *od*, larger than the inner, of massive, irregular form; inner style, *id*, strongly compressed, the beak small and relatively slender. Gonapophyses appearing as long and slender rods.

Holotype, ♂, Gothic, 9,500 ft., July 21, 1934 (J. D. Hallahan). *Allotopotype*, ♀, July 29, 1934 (Alexander). *Paratopotypes*, 4 ♂♂, July 17-19, 1934 (Alexander & Hallahan).

Tipula (*Bellardina*) *gothicana* is closest to *T. (B.) subcinerea* Doane, differing conspicuously from this and all other described species in the structure of the male hypopygium, especially the ninth tergite. Several large and handsome species of *Tipula* in the Rocky Mountain and Pacific Coast regions seem best referred to the subgenus *Bellardina* Edwards, 1931, although they differ in certain respects from the subgenotype of the last. These species include *T. (B.) albimacula* Doane, 1912; *T. (B.) commiscibilis* Doane 1912 (*contaminata* Doane, 1901, preoccupied); *T. (B.) faustina* Alexander, 1941; *T. (B.) pacifica* Doane, 1912; *T. (B.) pura* Alexander, 1941; *T. (B.) ramona* Alexander, 1941; *T. (B.) rupicola* Doane, 1912; and *T. (B.) subcinerea* Doane, 1901, among the described forms. In the Himalayan-Chinese fauna there is an almost equal development of large and showy species that have been placed in a special subgenus *Sinotipula* Alexander, 1935. With the recent accession of many new species in Tropical America it appears doubtful whether the last named group can be maintained as distinct from *Bellardina*.

Tipula (*Yamatotipula*) *albocaudata* Doane, 1901.—Gothic, 9,500 feet, near the river, July 2, 1934; above Gothic, 10,100 feet, along a small mountain stream, July 12, 1934. One male from Logan Cañon, Utah, May 28, 1938 (*Bischoff*) is considerably darker than the above specimens, especially in the wings, but from the structure of the male hypopygium is the same.

Whether *T. (Y.) cognata* Doane, 1901, will prove to be a synonym of the above is still in question.

Tipula (Yamatotipula) continentalis Alexander, 1941.—Gothic, 9,500 ft., July 4, 1934; 10,000 ft., July 12 and August 1, 1934. These specimens show the following range in size: ♂. Length about 12-14 mm.; wing, 13.5-16 mm. ♀. Length, about 16-18 mm.; wing, 15-16 mm.

I have seen other specimens from Three Sisters, Sunshine Shelter, Oregon, 6,000 ft., July 12, 1936 (*R. E. Rieder*); Oregon State College. These latter are even larger than the above, with the wing pattern more conspicuous, but from the structure of the male hypopygium are conspecific.

Tipula (Oreomyza) sarta Loew, 1863.—Gothic, 9,500 ft., July 18, 1934 (*Hallahan*); 11,000 ft., July 4, 1934 (*Hallahan*).

Tipula (Lunatipula) macrolabis Loew, 1864.—Gothic, 9,500 ft., July 23, 1934 (*M. M. A.*)

Tipula (Lunatipula) barbata Doane, 1901.—Originally described from 1 ♂ and 2 ♀♀, labelled only "Col.", collected by H. K. Morrison; type, U.S.N.M. 10,937. The species is now becoming better known and some further notes and figures concerning it are given.

♂. Length, about 10 mm.; wing, 11 mm.; antenna, about 4 mm.

Antennae with scape and pedicel yellow, flagellum uniformly dark brown; flagellar segments very feebly but scarcely incised, the basal swellings inconspicuous; verticils much shorter than the segments.

Mesonotal praescutum brownish gray with two narrow but conspicuous intermediate stripes, the usual lateral pair very poorly indicated; a darkened triangle just inside the humeral region; scutal lobes dark brownish gray, the median region paler; posterior sclerites of notum gray with a continuous capillary, dark brown, median vitta. Femora yellow, the tips somewhat broadly and conspicuously dark brown, the amount subequal on all legs; claws (male) toothed.

Male hypopygium (Figs. 2, 3) with the tergite, *9t*, produced cephalad along the lateral portions, the median length much shorter; caudal border with a deep U-shaped notch, the very broad lateral lobes truncated. Basistyle, *b*, on ventro-caudal portion with a conspicuous subglobular lobe that is provided with long setae, the more ventral ones longest, exceeding twice the diameter of the lobe, the dorsal setae small and delicate. Outer dististyle, *od*, a small pale lobe. Inner dististyle, *id*, a compact structure, the posterior lobe extensive but not well differentiated from the main body of style; dorsal crest pale, membranous, with longitudinally parallel ribs; beak of style short. Gonapophyses, *g*, appearing as darkened subcircular blades. Eighth sternite, *8s*, extensive sheathing, the lateral lobes bearing long conspicuous setae, especially the outer one of either side which rises from the summit of a short tubercle and is distinctly fasciculate, the remaining strong setae totalling about a dozen on either side, in a more or less evident row, their free tips decussate across the

median line; a glabrous median plate projects between the lateral lobes, its caudal border gently emarginate.

Alberta: Edmonton, September 5, 1925 (*Owen Bryant*).

Colorado: Gothic, 9,500 ft., August 2, 1934; Peaceful Valley, August 25 (*Cockerell*); Halfway House, Pikes Peak, September (*Cockerell*).

New Mexico: White Mountains, south fork of Eagle Creek, altitude about 8,000 ft., at light, August 15-18 (*C. H. T. Townsend*).

It seems evident that the species is a late summer and early fall form.

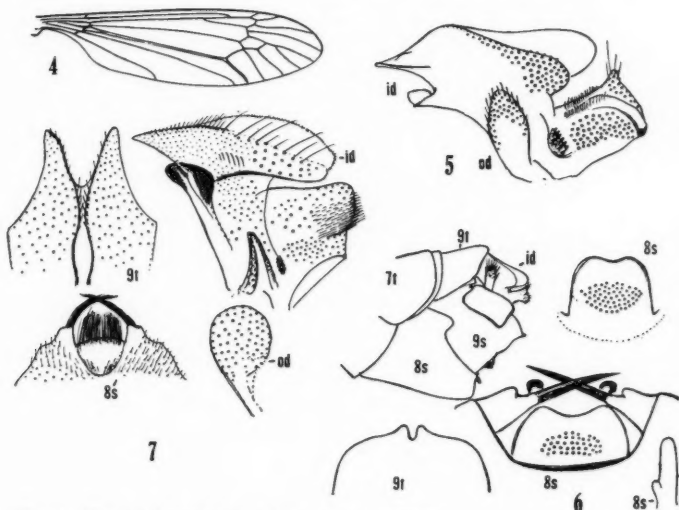


Fig. 4. *Tipula (Lunatipula) rabiosa* sp. n.; venation.

Figs. 5, 6. *Tipula (Lunatipula) rabiosa* sp. n.; male hypopygium.

Fig. 7. *Tipula (Lunatipula) bigeminata* Alexander; male hypopygium.

(Symbols: id, inner dististyle; od, outer dististyle; s, sternite; t, tergite.)

Tipula (Lunatipula) bigeminata Alexander, 1915.—Originally described from Nevada. Like the last, the fly is still insufficiently known and supplementary details are given.

Ovipositor with cerci very long and slender, almost straight. Male hypopygium (Fig. 7) with the tergite, *9t*, long and narrow, the lobes conspicuous, subparallel to weakly divergent, separated from one another by a deep U-shaped notch; dorsal face of tergite with a deep groove, the adjoining margins approximated on cephalic portion of sclerite and provided with setae. Outer dististyle, *od*, on outer half expanded into an unusually large, nearly circular spatula. Inner dististyle, *id*, complex, as shown; a conspicuous dorsal crest that becomes very pale and weakly fimbriate along the extreme margin; posterior

lobe of style broad. Basistyle with a strong lobe immediately ventrad of the point of insertion of the dististyles, this lobe blackened, its outer half cylindrical, provided with numerous short but very strong setae; above this lobe a powerful flattened reddish blade, the tip acute. Eighth sternite, $8s$, with the fasciculate bristles of lateral lobes decussate across median line; median lobe large and pale, fringed with long pale setae; more anteriorly the dorsal or inner surface, together with the inner faces of the lateral lobes provided with abundant strong curved reddish bristles.

Gothic, 9,500 ft., July 4, 1934; 10,000 ft., July 4-5, 1934; Kebler Pass, Colorado, 10,150 ft., July 15, 1934.

Tipula (Lunatipula) rabiosa sp. nov. — General coloration yellow, the praescutal stripes relatively indistinct; flagellar segments uniformly dark brown to brownish black; wings grayish yellow, the prearcular and costal fields light yellow; stigma pale brownish yellow; obliterative areas small and inconspicuous; male hypopygium with the tergal lobes low and obtuse; outer dististyle a short spatula; eighth sternite with a pair of very powerful spines crossing one another at the midline.

♂. Length, about 16-17 mm.; wing, 16-18 mm.; antenna, about 4-4.5 mm.

Frontal prolongation of head obscure yellow; nasus stout; palpi brown, the terminal segment brownish black. Antennae relatively short; scape and pedicel yellow, first flagellar segment light brown; remainder of flagellum dark brown to brownish black; flagellar segments only weakly incised; longest verticils subequal to or a little shorter than the segments. Head buffy yellow, sparsely pruinose; vertical tubercle poorly developed.

Mesonotal praescutum obscure yellow, the three stripes very poorly differentiated, the median one slightly more reddish; posterior sclerites of notum more reddish, with a yellow pollen, the scutal lobes and the scutellum slightly more darkened. Pleura yellow. Halteres with stem yellow, knob darkened, the apex slightly paler. Legs with coxae and trochanters obscure yellow; femora yellow, the tips narrowly dark brown, the amount subequal on all legs; tibiae and basitarsi obscure yellow, the latter darkened at tips; remainder of tarsi brownish black; claws (male) with a single strong tooth. Wings (Fig. 4) grayish yellow, the prearcular and costal fields, especially cell Sc , conspicuously light yellow; stigma pale brownish yellow; obliterative areas across cord very small and inconspicuous. Venation: R_{1+2} preserved; $m-cu$ fully two-thirds the length of Rs .

Abdominal tergites yellow, the second and succeeding segments with a conspicuous dark brown to black sublateral stripe; intermediate tergites with vague indications of a broken median stripe, most conspicuous as spots on segments four to six; sternites yellow; hypopygium reddish brown. Male hypopygium (Figs. 5, 6) relatively large, highly complex in structure; tergite, sternite and basistyle all completely separated by sutures; eighth sternite moderately sheathing, its sides near base with a conspicuous posterior extension; eighth tergite reduced to a narrow band. Ninth tergite, $9t$, relatively small, the

caudal margin convexly rounded, the median portion with a relatively small but deep U-shaped notch, the lateral lobes thus formed low and obtuse. Dististyles as figured, the outer style, *od*, a small flattened spatula. Outer portion of inner dististyle, *id*, produced caudad into a pale membranous flange or blade, the surface of which is microscopically wrinkled but without setae; posterior lobe of style complex, provided with abundant coarse and delicate setae and setulae; sensory group consisting of about a dozen triangular or conical spinous points. Ninth sternite with mesal arms jutting to the mid-ventral line, delicately fringed with golden yellow setae; sternite with caudal portion terminating in a small apiculate point. Eighth sternite, *8s*, with caudal end emarginate, on either side bearing a powerful reddish spine composed of fasciculate bristles, arising from a stout bilobed base, the two spines decussate across the median line; at base of emargination with a pale depressed median lobe or plate, the face of which bears numerous setae. Immediately above this median plate project the rounded ends of conspicuous paired rods arising from the basal portions of the eighth sternite.

Holotype, ♂, Gothic, 9,500 ft., July 7, 1934 (Alexander). *Paratopotypes*, 5 ♂♂, 9,500-10,600 ft., July 3-19, 1934 (Alexander & Hallahan).

The nearest relative of the present fly is *T. (L.) bigeminata* Alexander, 1915, previously discussed. The two species are well distinguished from one another by the coloration of the body and wings, and especially by the quite distinct male hypopygia. Throughout the Nearctic region there are several other members of the same group, all characterized by having large and unusually complex male hypopygia.

Nephrotoma altissima erythrophrys (Williston, 1893).—Gothic, 9,500 ft., July 1, 1934. From the studies of Professor J. Speed Rogers, it would appear that both *altissima* (Osten Sacken, 1877) and the present form will better be considered as representing forms of the more eastern *lugens* (Loew, 1864).

CYLINDROTOMINAE

Cylindrotoma pallescens Alexander, 1930.—Gothic, 9,500-10,000 ft., very numerous along streams at the latter altitude near upper edge of the Biological Forest. The exact relationships existing between *C. americana* Osten Sacken, 1865, *C. juncta* Coquillett, 1900, *C. splendens* Doane, 1900, and the present fly are still not thoroughly understood. It should be observed that in the present fly, the male is much darker in color than the pallid female.

LIMONIINAE LIMONIINI

Limonia (Limonia) indigena jacksoni (Alexander, 1917).—Described from Geneva Park, Grant, Colorado, 9,500-10,000 ft., July 16-22, 1916 (*L. O. Jackson*). Gothic, 9,500 ft., July 4, 1934; Kebler Pass, 10,100 ft., July 15, 1934 (Alexander). I am still uncertain as to whether the present fly should be considered as representing a valid species.

Limonia (Limonia) sciophila (Osten Sacken, 1877).—Gothic, 9,500 ft., July 2, 1934.

Limonia (Limonia) solitaria (Osten Sacken, 1859).—Gothic, 9,500 ft., July 4, 1934 (*M. M. A.*).

Limonia (Dicranomyia) ctenopyga sp. nov. — General coloration dark gray, the praescutum with a conspicuous median blackened stripe that is especially distinct in front; rostrum yellow; antennae black throughout; halteres with strongly infuscated knobs; femora obscure yellow, the tips narrowly and rather weakly infuscated; wings subhyaline, stigma brown, relatively conspicuous; Sc_1 long, only a little shorter than Rs ; cell $1st\ M_2$ relatively long, exceeding vein M_3 beyond it; male hypopygium complex; ninth tergite narrowly transverse, with an oval setiferous lobe at the midline; basistyle with the ventro-mesal lobe very large and conspicuous, near outer end with a single row or comb of flattened spinous setae; rostral spines two.

♂. Length, about 6.65 mm.; wing, 7.75 mm.

Rostrum yellow; palpi dark brown. Antennae black throughout; flagellar segments long-oval; terminal segment about one-third longer than the penultimate; longest verticils a little shorter than the segments. Head dark gray; anterior vertex relatively wide, fully twice the diameter of the scape.

Pronotum dark brown, gray laterally. Mesonotal praescutum dark gray, with a conspicuous median blackened stripe that is especially distinct in front, more obscured and pruinose behind; lateral stripes not or scarcely indicated; humeral region more ochreous pollinose. Pleura heavily gray pruinose, the dorsopleural region and the pleurotergite paler. Halteres of moderate length, stem obscure yellow, knob strongly infuscated. Legs with coxae brownish yellow, knob strongly infuscated. Legs with coxae brownish yellow, their outer surface sparsely pruinose; trochanters yellow; femora obscure yellow, the tips narrowly and rather weakly infuscated; tibiae and tarsi brown. Wings (Fig. 8) subhyaline; stigma brown, relatively conspicuous; prearcular field slightly yellowish; veins brown. Venation: Sc_1 ending about opposite origin of Rs , Sc_2 far from its tip, Sc_1 alone only a little shorter than Rs ; cell $1st\ M_2$ relatively long, exceeding in length vein M_3 beyond it; $m-cu$ close to fork of M ; vein $2nd\ A$ nearly straight.

Abdominal tergite brownish black, the incisures narrowly paler; sternites darkened basally, the posterior borders broadly pale; ninth segment and principal lobe of ventral dististyle pale, the remainder dark brown. Male hypopygium (Fig. 9) with the tergite, $9t$, unusually narrow and transverse, the lateral lobes correspondingly low, with scattered setae; an oval median lobe provided with about eight unusually long and conspicuous setae. Basistyle, b , with the body small, the ventro-mesal lobe very large and conspicuous, subequal in extent to the ventral dististyle; lobe elongate, somewhat pointed at outer end, before apex with an oblique ridge that is set with a row of conspicuous flattened spinous setae exceeding thirty in number. Dorsal dististyle with the basal third straight, the remainder gently curved, the apex a long

straight spine. Ventral dististyle, *vd*, with the rostral prolongation and its swollen base blackened, the apex of the prolongation a little produced; rostral spines two, relatively stout, placed close together at near one-third the length of prolongation; face of prolongation beyond the spines with about a dozen strong setae; swollen base of prolongation with long conspicuous setae, including a group of unusually long bristles on cephalic mesal portion. Gonapophyses, *g*, with mesal-apical lobe curved to an acute darkened point, the margin of lobe weakly crenate.

Holotype, ♂, Copper Creek below Judd Falls, 9,600 ft., July 6, 1934 (Alexander). *Paratopotypes*, 2 ♂♂, in the same place, August 2, 1934 (Alexander).

The most similar species is *Limonia (Dicranomyia) alascaensis* (Alexander, 1919), of Alaska, which is still known to me only from the unique type female. This latter differs in coloration, as the blackened rostrum and the color of the halteres, legs and abdomen, and in the venational details, as the arcuated *Rs* and short, subquadrate cell *1st M*₂. It seems certain that the male sex of *alascaensis*, when discovered, will show important hypopygial differences.

Limonia (Dicranomyia) gracilis (Doane, 1900).—Described from Idaho. Now known to have a wide distribution in the central Rockies. Gothic, 9,500-10,000 ft., July 18-August 1, 1934, the latter specimens in swampy areas along a small stream in the spruce-fir forest of the "Gothic Natural Area." This fly was often taken in company with *L. (D.) vulgata* (Bergroth, 1888).

Limonia (Dicranomyia) halterata (Osten Sacken, 1869).—This northern species was originally described from specimens taken in Labrador by Packard. It is now known to have a vast range across all northern North America,

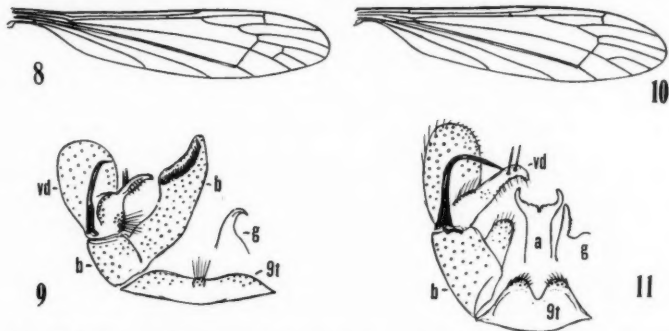


Fig. 8. *Limonia (Dicranomyia) clenopyga* sp.n.; venation.

Fig. 9. *Limonia (Dicranomyia) clenopyga* sp.n.; male hypopygium.

Fig. 10. *Limonia (Dicranomyia) vulgata* (Bergroth); venation.

Fig. 11. *Limonia (Dicranomyia) vulgata* (Bergroth); male hypopygium.

(Symbols: *a*, ædeagus; *b*, basistyle; *g*, gonapophysis; *t*, tergite; *vd*, ventral dististyle.)

extending southward along the higher Rockies and other mountain ranges. Gothic, 9,500 ft., July 4-12, 1934 (M. M. A.).

Limonia (Dicranomyia) morioides (Osten Sacken, 1860). — Another characteristic northern species having a distribution much like the last. Gothic, 9,500 ft., July 2-19, 1934, abundant.

Limonia (Dicranomyia) vulgata (Bergroth, 1888). — Allied to *immodesta*; general coloration yellow, more or less pruinose, the praescutum with three brown stripes; rostrum yellow; antennae black throughout; wings subhyaline, the stigma scarcely darker; Sc_1 long, exceeding one-half the length of R_s ; cell M_2 open by atrophy of m ; male hypopygium with the tergite conspicuously notched; lobe of basistyle simple; dorsal dististyle a slender, strongly curved hook; ventral dististyle fleshy, the rostral spines of moderate length; mesal face of main lobe of style with short spinous setae; mesal-apical lobe of gonapophysis slender and straight, the outer margin microscopically serrulate; aedeagus terminating in conspicuous sclerotized points.

♂. Length about 6-6.5 mm.; wing, 6.5-7.2 mm.

Rostrum yellow; palpi brownish black. Antennae black throughout; flagellar segments passing through short-oval to long-oval, the terminal segment exceeding the penultimate in length; verticils long and conspicuous, exceeding the segments. Head gray, the vertex more or less infuscated medially; anterior vertex wide, approximately three times the diameter of scape.

Pronotum dark brown above, the lateral borders yellow. Mesonotal praescutum yellow, more or less pruinose, with three brown to brownish black stripes, the median one wider and more intense, not reaching the suture behind, the lateral stripes more pruinose; central portion of scutum and scutellum yellow, the lateral portions dark brown, more or less pruinose, parascutella pale; mediotergite darkened on central portion, broadly yellow on sides. Pleura and pleurotergite yellow, with a whitish pruinosity, the pleurotergite a trifle more darkened. Halteres elongate, stem yellow, knob darkened. Legs with the coxae and trochanters yellow; femora obscure yellow, the tips weakly darkened; tibiae brownish yellow; tarsi passing through brown to black. Wings (Fig. 10) subhyaline, unpatterned; stigma varying in intensity, in cases scarcely differentiated from the ground, in other cases pale brown; veins brown, prearcular veins and Sc more yellow. Venation: Sc short, Sc_1 ending opposite or shortly before origin of R_s , Sc_2 some distance from its tip, Sc_1 alone exceeding one-half the length of R_s ; cell M_2 open by the atrophy of m ; $m-cu$ close to fork of M .

Abdomen dark brown, the basal sternites more brightened; eighth segment and ninth tergite pale, the basistyles more darkened. Male hypopygium (Fig. 11) with the tergite, $9t$, deeply notched medially, the relatively narrow lobes densely provided with blackened setae that are directed strongly mesad. Basistyle, b , with the ventro-mesal lobe relatively small, simple, with abundant but pale and delicate setae. Dorsal dististyle an unusually long and slender

curved hook, gradually narrowed to the subacute apex. Ventral dististyle, *vd*, pale and fleshy, the mesal face of the main lobe with short spinous setae, those of the outer face much longer and more conspicuous; a row of long setae along base of prolongation; prolongation conspicuous, curved and flattened; rostral spines two, separate at their bases, a little longer than the prolongation beyond the outer spine. Gonapophyses, *g*, with mesal-apical lobe slender, straight, darkened, the tip subacute, the margin back from the tip microscopically serrulate. Aedeagus, *a*, stout, the outer lateral angles produced into conspicuous sclerotized points.

♂, Gothic, 10,000 ft., July 12, 1934 (Alexander); ♂♂, 9,500 ft., July 18, 1934 (Alexander). The first were taken along streams in the spruce-fir forest near the upper edge of the "Gothic Natural Area," associated with *L. (D.) gracilis* (Doane) and other crane-flies; the latter were swept from swampy areas among small beaver dams near the bridge at Gothic, again associated with *gracilis*.

Limonia (Dicranomyia) vulgata is amply distinct from the three most closely allied species, *L. (D.) gladiator* (Osten Sacken, 1859), *L. (D.) immodesta* (Osten Sacken, 1859), and *L. (D.) iowensis* (Rogers, 1926). The structure of the male hypopygium is distinctive, especially the ventral dististyle, with its prolongation, the gonapophyses, and the aedeagus. Among the relatives above listed, it is most similar to *L. (D.) immodesta*. The shortened spinous setae on the mesal face of the ventral dististyle are quite different from those in these related species though somewhat similar to the condition found in the otherwise quite different *L. (D.) modesta* (Wiedemann, 1818).

Antocha (Antocha) monticola Alexander, 1917. — Gothic, along East River, 9,500 ft., July 10, 1934.

Elliptera astigmatica Alexander, 1912.—Described from British Columbia; known hitherto from the northern Rockies of the United States and Canada. The present records are the most southerly so far made known. Gothic, 10,450-10,600 ft., July 12-19, 1934; especially common near Emerald Lake where they were found resting on the rock faces of small cliffs or occurring in small crannies, with no water present. In the male sex, a surprising range in the size and modification of the radial field of the wing is found, not only in the present species but in others in the same genus throughout the entire Holarctic region. In the present small series, the males show a wing length between 10 and 14.5 mm. In some specimens, the enlargement of the outer radial cells is accompanied by a deepening in color, and, in cases, with a weak spur of a vein near the outer end of cell R_1 , arising from vein R_3 ; in addition, some specimens show weak traces of R_2 , shortly beyond the fork of R_5 . In still other individuals, the normally closed cell $1st\ M_2$ tends to be open by the partial atrophy of the outer deflection of vein M_3 . One specimen, a small male, shows the surprising anomaly of total loss of *m-cu* in both wings; normally this lies from about one-half to its own length before the fork of M , in rarer cases, closer to the fork. In most specimens, the basal section of

R_{4+5} is arcuated to very weakly angulated. The character of R_s usually being equal in length to or longer than its anterior branch in *astigmatica* while being shorter than this branch in *coloradensis* does not hold in a series of specimens.

The three Western Nearctic species of *Elliptera* may be separated as follows:

1. Stigma distinct, oval, brown; vein R_{2+3} immediately beneath the stigma bent strongly caudad, beyond the stigma regaining its former level. (California).....*clausa* Osten Sacken, 1877
No well-delimited stigmal darkening; vein R_{2+3} straight or virtually so 2
2. Wings distinctly patterned, with evident brown seams along cord and outer end of cell 1st M_2 . (Colorado)*coloradensis* Alexander, 1920
Wings without dark seams along cord or outer end of cell 1st M_2 . (British Columbia, Wyoming, Colorado).*astigmatica* Alexander, 1912.

Elliptera coloradensis Alexander, 1920. — Described from the Rocky Mountain National Park, Colorado. Gothic, 9,500 ft., July 19-27, 1934; 1 ♂, 10,450 ft., July 12, 1934. The larvae occurred on vertical board walls at the falls of East River above the old saw-mill. They lived where the wood was constantly wetted by thin sheets of water trickling over them, mostly quite exposed but some in flimsy cases composed of silk covered with silt. The adult flies rested on these same walls, often associated with *Erioptera* (*Ilisia*) *hygropetrica* sp. nov. The species is apparently best differentiated by the distinctly patterned wings, as described; in addition, the basal section of R_{4+5} is strongly angulated and often conspicuously spurred, the spur jutting backward into cell R . In most individuals, $m-cu$ is closer to the fork of M than in *astigmatica*. Although cell 1st M_2 is normally closed in all three of our western species of *Elliptera*, several specimens in the present series showed the cell open by the atrophy of both m and the basal section of vein M_3 , leaving the outer section of the latter vein stranded in the membrane, much as in the net-winged midges, *Blepharoceridae*.

PEDICIINI

Pedicia (*Tricyphona*) *aspidoptera* (Coquillett, 1905).—This surprising fly was originally described as a *Limnophila*, with a question, by Coquillett. The next year (*Ent. News*, 17:29, fig. of adult male; 1906) the species was definitely assigned to *Limnophila*, as it was in a still later reference (Alexander, *Can. Ent.* 49:208, pl. 12, fig. 9, wing; 1917).

The species was described from material taken on the summit of the Las Vegas Mountains, New Mexico, taken on June 29th, by Cockerell (Type, U.S.N.M. 9033). Other specimens were taken at high altitudes in the Rockies near Beulah, New Mexico, by H. L. Viereck, presumably a locality identical with the type station. Rather numerous specimens representing both sexes, from Gothic and the adjoining slopes of Gothic Mountain, 9,500-10,000 ft., July 3-5, 1934 (Alexander). As indicated by all previous references, the species is subapterous in both sexes, more resembling a large spider or phalangid when noted alive. Despite the almost wingless condition, almost all

specimens taken were swept from tall herbs where the flies had walked or climbed to a height of two or three feet.

A study of this material shows that the fly is not a *Limnophila* (Hexatmini) but a true *Tricyphona*, belonging to the Pediciini. The eyes are not glabrous, as described by Coquillett but the setae between the ommatidia, while of normal size, are very sparse and scattered, as evidenced by their punctures. The halteres are always slightly longer than the wings, as shown by the following measurements:

♂. Length, about 11-13 mm.; wing, about 1-1.2 mm.; halteres, 1.5-1.7 mm.

♀. Length, about 16-18 mm.; wing, about 1.4-1.6 mm.; halteres, 1.8-2 mm.

The male hypopygium (Fig. 16) indicates that the fly belongs to the *ampla* group, represented by a few species in both the eastern and western Nearctic region. Ninth tergite, *9t*, with the caudal margin subtruncate to very gently rounded, the surface with numerous long pale setae. Apex of basistyle, *b*, with numerous long coarse setae. Outer dististyle a small pale lobe at base of the inner style, provided with elongate setae that exceed in length the lobe itself. Inner dististyle, *d*, 5-lobed, as in the group; two innermost lobes longest, appearing as flattened blades with obtuse tips, their apices with microscopic setulae; innermost lobe with the most basal setae longer and more conspicuous; outer lobes shorter, two of them more pointed at their tips.

Among the Pediciini of the Nearctic fauna, as now known, there are several species showing brachypterism or stenopterism in the female sex or in both sexes. Besides the cases listed below, representing previously described species, I have still other undescribed forms, including one in the genus *Polyangaeus* Doane. The species described as *Limnophila nemoptera* Alexander, 1927, is still known only from the female sex. It will probably be found to be a Pediciine type, possibly a *Dicranota*.

Pedicia (Tricyphona) aspidoptera (Coquillett, 1905).—Western United States. Brachypterous in both sexes, wings very reduced.

Pedicia (Tricyphona) autumnalis (Alexander, 1917).—Eastern United States and Canada. Female only with slightly reduced wings.

Pedicia (Tricyphona) degenerata (Alexander, 1917).—Western North America. Both sexes showing moderate reduction of wings; see next species in this paper.

Pedicia (Tricyphona) hannai (Alexander, 1923).—Arctic North America, Pribilof Islands, Alaska. Both sexes strongly brachypterous.

Pedicia (Tricyphona) subaptera (Alexander, 1917).—Western United States. Wings moderately reduced in both sexes, exceeding the halteres.

Pedicia (Nasiternella) hyperborea (Osten Sacken, 1861).—Arctic and northern North America. Wings of female only very reduced.

Dicranota (Plectromyia) stenoptera (Alexander, 1927).—Western United States; both sexes with wings reduced to linear strips, stenopterous; discussed later in this paper.

Pedicia (Tricyphona) degenerata (Alexander, 1917).—Described from Geneva Park, Grant, Colorado, 9,500-10,000 ft., July 22, 1916 (E. C. Jackson). Gothic, 9,500-10,000 ft., July 5-18, 1934.

The normal venation and wing shape are as figured (Fig. 12); in even more degenerate individuals, cell M_1 may be lost by atrophy or fusion of the veins concerned (Fig. 13). It seems certain that the present fly represents a distinct species, differing from its nearest ally, *P. (T.) aperta* (Coquillett, 1905), by the coloration of the body, the reduced wings, with correlated changes in venation, and in details of structure of the male hypopygium.

Dicranota (Rhaphidolabis) cayuga (Alexander, 1916).—Wide-spread over northern North America. Gothic, 9,500 ft., July 2, 1934.

Dicranota (Rhaphidolabis) integriloba sp. nov. — General coloration gray, the praescutum with three more or less distinct brown stripes; antennae 15-segmented; halteres with knobs weakly infuscated; legs pale brown; wings whitish subhyaline, stigma very slightly darker; R_{2+3+4} longer than the basal section of R_5 ; abdomen brown with a brownish black subterminal ring, hypopygium yellow; male hypopygium with the tergite produced into a conspicuous median lobe that is slightly expanded outwardly, its caudal margin trun-

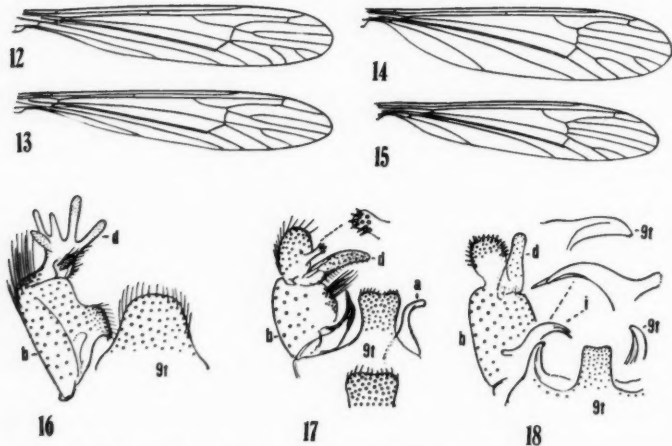


Fig. 12. *Pedicia (Tricyphona) degenerata* (Alexander); normal venation.
 Fig. 13. *Pedicia (Tricyphona) degenerata* (Alexander); abnormal venation.
 Fig. 14. *Dicranota (Rhaphidolabis) integriloba* sp. n.; venation.
 Fig. 15. *Dicranota (Plectromyia) engelmannia* sp. n.; venation.
 Fig. 16. *Pedicia (Tricyphona) aspidoptera* (Coquillett); male hypopygium.
 Fig. 17. *Dicranota (Rhaphidolabis) integriloba* sp. n.; male hypopygium.
 Fig. 18. *Dicranota (Plectromyia) engelmannia* sp. n.; male hypopygium.
 (Symbols: a, ædeagus; b, basistyle; d, dististyle; t, tergite.)

cate or but weakly emarginate.

♂. Length, about 7-7.5 mm.; wing, 6.5-7.5 mm.

Rostrum obscure brownish yellow; palpi brownish black. Antennae of moderate length, 15-segmented; flagellar segments short suboval or subcylindrical, the outer segments even more crowded; terminal segment shorter than the penultimate; verticils shorter than the segments. Head dark gray.

Thorax gray, the praescutum with three brown stripes that vary in intensity from pale to dark brown, the median one longer and broader; scutal lobes with brown centers; scutellum and posterior margins of scutal lobes yellow; postnotum gray. Pleura pale gray. Halteres with stem yellow, knob weakly infuscated. Legs with coxae and trochanters yellow; remainder of legs pale brown. Wings (Fig. 14) whitish subhyaline; stigma very slightly indicated; veins pale brown. Venation: R_{2+3+4} from one and one-half to two times the basal section of R_5 ; cell M_1 about one-half as deep as cell M_3 .

Abdomen brown, with a more brownish black subterminal ring involving segments seven and eight; hypopygium abruptly and conspicuously yellow. Male hypopygium (Fig. 17) with the median tergal lobe, $9t$, long and conspicuous, only slightly widened outwardly, the caudal margin subtruncate to weakly emarginate, the lateral angles obtusely rounded, inconspicuous. Mesal face of basistyle, b , with a row of very long setae that are arranged more or less evidently into two or three groups; interbase broad at base, narrowed to a long acute point. Outer dististyle, od , with a cylindrical spine-tipped appendage on face. Inner dististyle an elongate, compressed blade, the tip obtuse. Aedeagus, a , a stout dusky lobe that is bent at a right angle at near midlength, the apex obtusely rounded.

Holotype, ♂, Gothic, 9,500 ft., July 6, 1934 (Alexander). *Paratopotypes*, ♂♂, 9,500-9,600 ft., July 6-August 2, 1934 (Alexander).

Dicranota (*Rhaphidolabis*) *integriloba* is quite distinct from the other generally similar regional species of the subgenus. The type of male hypopygium is different from other species of the subgenus, being more like that found in species of the related subgenus *Plectromyia* Osten Sacken, as *petiolata* (Alexander), *engelmannia* sp. nov., and *stenoptera* (Alexander). The male sex of *D. (R.) major* (Alexander) and *D. (R.) sessilis* (Alexander) are still unknown but from the coloration and venation the present fly cannot be referred to either of these flies.

Dicranota (*Plectromyia*) *petiolata* (Alexander, 1919).—Gothic, 10,000 ft., along a small clear stream in the "Gothic Natural Area," August 1, 1934; 10,100 ft., on trail to Emerald Lake, along a small mountain torrent, July 12, 1934.

Dicranota (*Plectromyia*) *stenoptera* (Alexander, 1927). — Originally described as a species of *Tricyphona* but from the structure of the male hypopygium certainly a member of this genus and presumably of *Plectromyia*. The wings of both sexes are reduced to linear strips so that the venation is distorted

beyond any taxonomic use. In the present specimens, the wings are slightly longer than in the type, with the venational details a little more evident. Gothic, 9,500 ft., in swampy areas near the beaver dams on East River near bridge, July 18, 1934; 10,500 ft., in wet spots on slopes of Gothic Mt., July 19, 1934 (Hallahan).

Dicranota (Plectromyia) engelmannia sp. nov. — Size small (wing, male, 4.5 mm.); general coloration ochreous or brownish yellow; head gray; wings with a pale yellow or milky tinge, the veins very pale to scarcely visible; cell R_3 short-petiolate; male hypopygium with the median region of tergite produced caudad into a rectangular lobe that is nearly parallel-sided, its apex truncate or virtually so.

♂. Length, about 4.4-5 mm.; wing, 4.5 mm.

♀. Length, about 5.5 mm.; wing, 5.5 mm.

Rostrum pale; palpi black. Antennae brownish black; flagellar segments oval, the outer segments smaller. Head gray.

Thorax almost uniformly ochreous or brownish yellow, the praescutum a little darker, slightly pruinose; thorax narrow, the praescutum produced cephalad. Halteres pale, apex of knob dark brown. Legs with the coxae and trochanters yellow; legs dark brown, the proximal portions of femora and basitarsi restrictedly pale; legs relatively long and slender. Wings (Fig. 15) small, with a pale yellow or milky tinge, the veins very pale to scarcely visible against the ground; no stigma or other darkened pattern. Sparse macrotrichia on veins beyond cord. Venation: Sc_1 ending just beyond fork of R_{2+3+4} ; Sc_2 not evident; R_s strongly arcuated to feebly angulated at near midlength; R_{2+3+4} about equal in length to the basal section of R_5 ; R_2 subequal to R_{1+2} ; cell M_3 much shorter than its petiole, in cases only about one-half to one-third its length beyond fork of M ; cell 2nd A relatively wide.

Abdomen brownish yellow to pale brown, in male with a narrow, darker brown subterminal ring; hypopygium clear yellow. Male hypopygium (Fig. 18) of the general type of structure of *petiolata*. Ninth tergite, $9t$, with the median area produced into a rectangular lobe, nearly parallel-sided and with the apex truncate or with a very shallow notch; outer lobes of tergite appearing as simple flattened blades, their tips subacute, slightly arcuated and microscopically denticulate at tips. Basistyle, b , with the apical lobe broad, provided with abundant spinulae; interbase, i , slender, at apex split into two slender points, one a little longer and more acute than the other. Dististyle, d , narrowed outwardly, the tip obtuse.

Holotype, ♂, Biological Forest, above Gothic, 10,000 ft., August 1, 1934 (Alexander). *Allotopotype*, ♀, mounted with type. *Paratopotypes*, 8 ♂ ♀. These specimens occurred in swampy areas along a small clear stream flowing through the spruce-fir forest. Associated with *Dicranota (Plectromyia) petiolata* (Alexander), *Limonia (Dicranomyia) gracilis* (Doane), *L. (D.) vulgata* (Bergroth), and others mentioned in this report.

The nearest relatives are *Dicranota* (*Plectromyia*) *petiolata* and *D. (P.) reducta* (Alexander), both of which differ conspicuously in the structure of the male hypopygium. In the conformation of the median tergal lobe, the present fly is more like *reducta* but the other structures are different.

HEXATOMINI

***Limnophila* (*Elaeophila*) *aldrichi alticrista* subsp. nov. —**

♂. Length, about 7.5 mm.; wing, 8 mm.

♀. Length, about 8.5 mm.; wing, 9 mm.

Differs from typical *aldrichi* Alexander, 1927, from the northern Rocky Mountains (Alberta, Montana) chiefly in the details of structure of the male hypopygium, especially the very high crest of the outer dististyle (Fig. 25, *od*). In the typical form, the style is proportionately narrower and the crest is low and relatively inconspicuous (Proc. U.S. Nat. Mus., 72, art. 2, pl. 1, fig. 6; 1927).

L. (E.) angustior Alexander, 1919, of Colorado to Montana, has the structure of the male hypopygium quite distinct, the apex of basistyle being provided with numerous, very long, yellow setae that exceed in length the longest dististyle. Outer dististyle long and narrow, its apical point relatively small.

Holotype, ♂, Gothic, 9,500 ft., July 6, 1934 (*Alexander*). *Allotopotype*, ♀, 9,800 ft., July 8, 1934. *Paratopotypes*, ♂ ♀, 9,800 ft., July 3, 1934; 10,100 ft., July 12, 1934.

Limnophila (*Phylidorea*) *claggi* Alexander, 1930.—Gothic, 9,800-10,100 ft., in swampy areas, July 3-12, 1934. The nearest relative is *L. (P.) subcostata* (Alexander, 1911), of northeastern North America, well-distinguished by the gray coloration instead of the polished black of the present fly.

Limnophila (*Phylidorea*) *platyphallus* Alexander, 1926.—Gothic, 9,500 ft., July 7, 1934. Widespread throughout northeastern and northern North America. Although allied to the European *L. (P.) fulvonervosa* (Schummel, 1829), the present fly is amply distinct.

Limnophila occidens Alexander, 1924.—Gothic, 9,800 ft., July 3-10, 1934; common in the special study area on the slopes of Gothic Mt. and along the East River. Swarming among the Engelmann's Spruce, usually in groups of from three to ten. Also taken at Monarch Pass, Colorado, 10,500 ft., July 1, 1934; swept from among the spruce and firs near the crest of the pass. This is the largest known species of the *nemoralis* (*brevifurca*) group, with numerous representatives in Europe and eastern Asia, together with the much smaller *L. brevifurca* Osten Sacken, 1859, of northeastern and eastern North America.

Shannonomyia oslari (Alexander, 1916).—Gothic, 9,500-10,100 ft., July 2-12, 1934; Monarch Pass, 10,500 ft., July 1, 1934. Widespread throughout the central Rockies.

Hexatoma (Eriocera) eriophora (Williston, 1894).—Gothic, 9,500-10,000 ft., July 7-12, 1934. Williston's types were from Washington State. The present material has the antenna of male a little shorter than in the type (8 mm.) but in other regards the specimens agree sufficiently well with the description and other determined material in my collection.

♂. Length, about 16-17 mm.; wing, 16-18 mm.; antenna, 7-7.5 mm.

♀. Length, about 23-24 mm.; wing, 19 mm.; antenna, about 5 mm.

ERIOPTERINI

Gonomyia (Idiocera) gothicana sp. nov. — General coloration yellow, variegated with dark brown; thoracic pleura striped with yellow and brown, the dorsal dark stripe not involving the pteropleurite; wings yellowish gray, unpatterned except for the vaguely darkened stigma; Sc_1 very long; male hypopygium with both the intermediate dististyle and inner dististyle bifid; aedeagus with three strong black spines near apex, the larger more basal spine directed strongly cephalad.

♂. Length, about 6-6.5 mm.; wing, 6.5-6.8 mm.

Rostrum pale yellow; palpi black. Antennae with the scape yellow above, darker beneath; remainder of antennae black; flagellar segments oval, the outer segments becoming more elongate. Head light yellow, the posterior portion and a median line on vertex brown; anterior vertex broad.

Pronotum brownish gray, the lateral margin narrowly yellow; pretergites yellow. Mesonotal praescutum brownish gray, the humeral and lateral portions abruptly light yellow; posterior sclerites of notum darkened, the scutellum not or scarcely brightened; mediotergite with lateral margin narrowly yellow, the pleurotergite more extensively brightened, the ventral margin brown. Pleura light yellow, variegated longitudinally with brown, including a dorsal stripe from the propleura across the anepisternum, not including the pteropleurite which is uniformly pale; a fainter and more restricted brown darkening on the ventral sternopleurite and meron. Halteres relatively long, stem obscure yellow, knob weakly darkened. Legs with the coxae and trochanters yellow; remainder of legs obscure yellow, the tips of tibiae narrowly and vaguely darkened; outer tarsal segments more blackened. Wings (Fig. 19) yellowish gray subhyaline, unpatterned except for the pale brownish yellow stigma that is only a trifle darker than the ground; prearcular and costal fields more yellow, including the veins; remaining veins pale brown, delicate. Venation: Sc long, Sc_1 ending about opposite one-half to four-fifths the length of R_s , Sc_2 far from its tip, opposite the origin of R_s or only slightly beyond, Sc_3 alone subequal to or exceeding the petiole of cell R_3 ; R_s elongate, arcuated at origin; faint indications of vein R_2 at proximal end of stigma; veins R_{1+2} and R_3 only narrowly separated at wing margin; $m-cu$ much more than its own length before fork of M .

Abdominal tergites dark brown, the lateral borders narrowly, the posterior

margins more broadly pale, becoming more extensive on the outer segments, especially the eighth; sternites and hypopygium chiefly pale. Male hypopygium (Fig. 27) with the outer dististyle, *od*, a slender simple rod, the acutely pointed distal fourth blackened. Intermediate dististyle, *md*, without setae, longer than the other styles, bifid, the outer arm slender, narrowed to a long acute point; shorter arm darkened, less than one-half the length of the outer arm. Inner dististyle, *id*, profoundly bifid, the outer arm a slender pale spine, its acute apex blackened; inner arm shorter but stouter, provided with sparse delicate setulae. Apical lobe of basistyle, *b*, relatively long, extended caudad about to the outer end of the outer dististyle, provided with numerous long setae. Aedeagus, *a*, a stout rod, near apex produced into a recurved blackened spine, with two smaller spines still closer to tip.

Holotype, ♂, Gothic, 9,500 ft., July 11, 1934 (Alexander). *Paratopotypes*, 2 ♂♂, July 2, 1934 (Alexander).

Gonomyia (Idiocera) gothicana is very different from all other regional members of the subgenus, especially in the structure of the male hypopygium, notably the dististyles and aedeagus. In the armature of the latter the species is approached only by *G. (I.) mathesoni* Alexander, of northeastern North America, which is otherwise an entirely different fly. In the structure of the male hypopygium, the species is closer to the eastern Palearctic *G. (I.) pallens* Alexander, 1928, and *G. (I.) perpallens* Alexander, 1938, which differ chiefly in relatively minor details of structure of the dististyles.

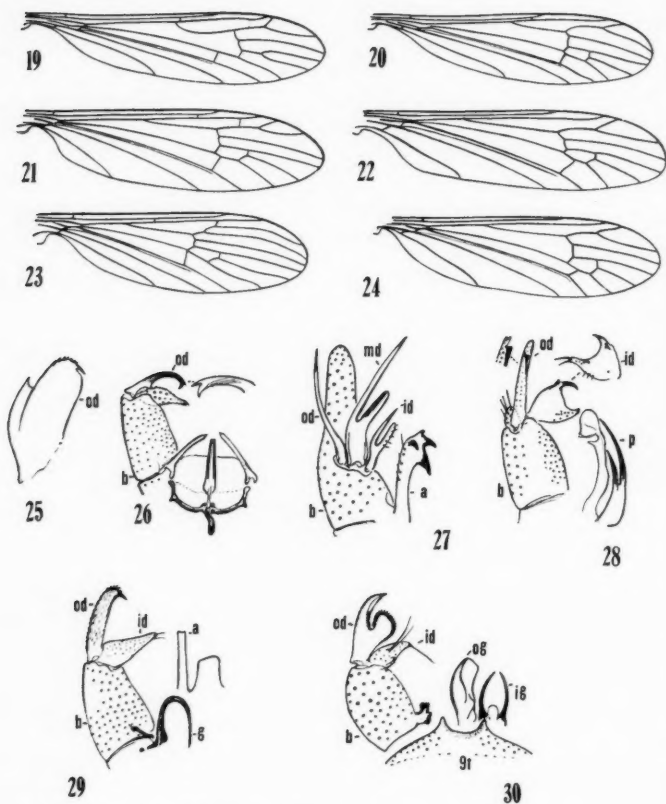
Gonomyia (Gonomyia) extensivena sp. nov. — General coloration yellow, patterned with dark brown; rostrum yellow; antennae entirely black, the outer flagellar segments elongate; head dark gray; scutellum yellow; central region of scutum and lateral portions of mediotergite extensively yellow; pleura chiefly yellow, restrictedly patterned with darker; knobs of halteres infuscated; legs brownish black to black; wings grayish subhyaline, stigma very slightly darker; *Sc* long to very long, *Sc*₁ ending from one-fifth to approximately one-half the length of *Rs*; *m-cu* just beyond fork of *M*; male hypopygium with the outer dististyle slender, straight, with a narrow blackened flange before apex; inner dististyle a compressed blade, bearing a long curved spine, with a smaller lateral spine on its face; phallosome with two unequal black spines and a longer compressed blade of irregular conformation.

♂. Length, about 5.8-6 mm.; wing, 6.5-6.7 mm.

♀. Length about 6.5 mm.; wing, 6.5 mm.

Rostrum varying from light sulphur yellow to more obscure yellow; palpi black. Antennae black throughout, relatively elongate; outer flagellar segments very elongate-oval to subcylindrical, the outer segments exceeding the verticils in length. Head dark gray.

Pronotum and pretergites light yellow, the scutellum narrowly and vaguely darkened medially. Mesonotal praescutum dark brownish gray, the lateral and

Fig. 19. *Gonomyia (Idiocera) gothicana* sp. n.; venation.Fig. 20. *Gonomyia (Gonomyia) extensivena* sp. n.; venation.Fig. 21. *Rhabdomastix (Sacandaga) leptodoma* sp. n.; venation.Fig. 22. *Rhabdomastix (Sacandaga) neolurida* sp. n.; venation.Fig. 23. *Erioptera (Ilisia) hygropetrica* sp. n.; venation.Fig. 24. *Rhabdomastix (Sacandaga) neolurida setigera* subsp. n.; venation.Fig. 25. *Limnophila (Elaeophila) aldrichi alticrista* subsp. n.; male hypopygium.Fig. 26. *Rhabdomastix (Sacandaga) leptodoma* sp. n.; male hypopygium.Fig. 27. *Gonomyia (Idiocera) gothicana* sp. n.; male hypopygium.Fig. 28. *Gonomyia (Gonomyia) extensivena* sp. n.; male hypopygium.Fig. 29. *Rhabdomastix (Sacandaga) neolurida* sp. n.; male hypopygium.Fig. 30. *Erioptera (Ilisia) hygropetrica* sp. n.; male hypopygium.

(Symbols: a, aedeagus; b, basistyle; g, gonapophysis; id, inner dististyle; ig, inner gonapophysis; md, intermediate dististyle; od, outer dististyle; og, outer gonapophysis; p, phallosome; t, tergite.)

humeral portions broadly light yellow, the central region restrictedly brightened at the suture; scutum yellow, the lobes extensively brownish gray, the dark color continued across the mid-line at the posterior portion of the scutum; scutellum broad, light yellow; mediotergite brownish gray, the cephalic-lateral portions broadly yellow; pleurotergite yellow, the ventral portion darkened. Pleura chiefly yellow, the ventral sternopleurite and meron abruptly darkened; a small dark cloud on anepisternum, not forming a longitudinal stripe. Halteres relatively elongate, stem yellow, knob infuscated. Legs with coxae more or less infuscated; trochanters brownish yellow; remainder of legs brownish black to black, the femoral bases more or less obscure yellow. Wings (Fig. 20) grayish subhyaline, the oval stigma very slightly darker, ill-delimited; prearcular and costal fields slightly more yellow, including the veins; remaining veins brown. Costal fringe relatively short. Venation: *Sc* unusually long for a member of this genus, *Sc*₁ ending from about opposite one-fifth to fully one-half the length of *Rs*, *Sc*₂ a short distance from its tip; *R*₂₊₃₊₄ elongate, gently arcuated, about four-fifths the length of *Rs* and fully twice *R*₃; *m-cu* just beyond fork of *M*.

Abdominal tergites dark brown, the incisures and lateral borders yellow; sternites yellow; hypopygium uniform yellow except for the blackened styli and apophyses. Male hypopygium (Fig. 28) with the apical lobe of basistyle, *b*, small and oval, pale. Outer dististyle, *od*, a slender elongate lobe, before apex bearing a narrow blackened flange. Inner dististyle, *id*, a compressed blade, the outer margin and angle produced into a curved blackened spine that bears a smaller tooth or flange on its face near base; rostral prolongation of style relatively slender, bearing the two usual fasciculate setae. Phallosome, *p*, consisting of an elongate flattened yellow blade of irregular conformation and two slender blackened spines, one much shorter and more slender than the other.

Holotype, ♂, Gothic, 10,100 ft., July 12, 1934 (Alexander). *Paratopotypes*, ♂ ♀, 9,500 ft., July 31, 1934 (Alexander). The types were collected along a small mountain stream on the trail to Emerald Lake; the paratype and other material from swampy areas near the beaver dams at Gothic.

Gonomyia (*Gonomyia*) *extensivena* is readily told from all other described regional species of the genus by the elongate *Sc*. In other forms, this vein ends opposite or before the origin of *Rs*. The structure of the male hypopygium is likewise distinctive.

Gonomyia (*Gonomyia*) *flicauda* Alexander, 1916.—Gothic, 9,500-10,000 ft., July 2-August 3, 1934, abundant.

Gonomyia (*Gonomyia*) *poliocephala* Alexander, 1924.—Gothic, 9,500 ft., July 31, 1934.

Rhabdomastix (*Sacandaga*) *leonardi* Alexander, 1930.—The species was originally described from Montana; now known to be widely distributed in the northern and central Rocky Mountains. The unique type was preserved in

alcohol and the normal pruinosity lost; as surmised at the time of the original description, in fresh specimens the dark coloration is more or less obscured by a gray bloom. Gothic, 9,500 ft., July 7, 1934; swept from low vegetation along the East River.

Rhabdomastix (Sacandaga) leptodoma sp. nov. — General coloration gray, the praescutum without clearly indicated praescutal stripes, halteres uniformly pale yellow; legs brownish black, the femoral bases yellow; wings subhyaline, the base narrowly pale yellow; stigma oval, pale brown; Sc_1 ending about opposite fork of R_s , R_2 weakly preserved, at about midlength of petiole of cell R_3 ; cell $1st\ M_2$ rectangular, $m-cu$ about one-half its length beyond the fork of M ; male hypopygium with the outer dististyle slender, bidentate at apex; gonapophyses long and narrow, even more slender than the aedeagus.

♂. Length, about 4.4.2 mm.; wing, 4.8.5 mm.

Rostrum and palpi black. Antennae short, black, the scape pruinose; flagellar segments oval to long-oval, the longest verticils exceeding the segments in length. Head dark gray; vertex broad.

Pronotum gray; anterior lateral pretergites almost white. Mesonotum and pleura uniform light gray, the praescutal stripes not or scarcely indicated; scutellum a trifle brightened. Halteres uniformly pale yellow. Legs with the coxae obscure brownish yellow or testaceous yellow, the fore pair somewhat darker; trochanters obscure yellow; remainder of legs dark brown to brownish black, the femoral bases yellow. Wings (Fig. 21) subhyaline, the base narrowly pale yellow; stigma oval, pale brown, ill-delimited; veins brown, yellow at the wing base. Venation: Sc_1 ending opposite or just before the fork of R_s , Sc_2 a short distance from its tip; R_2 preserved as a weak element at or just beyond midlength of petiole of cell R_3 ; vein R_3 oblique, cell R_3 relatively small; cell $1st\ M_2$ rectangular; $m-cu$ about one-half its length beyond the fork of M ; vein $2nd\ A$ nearly straight, the cell of moderate width only.

Abdomen black, heavily gray pruinose; base of hypopygium a little brightened, the styli dark. Male hypopygium (Fig. 26) of the general type of *monticola*. Outer dististyle, *od*, much more slender and less flattened, conspicuously bidentate at apex but with other denticles or points lacking or reduced to vague roughenings on the lower margin before the ventral spine. Apex of inner dististyle narrowed. Gonapophyses, *g*, longer and narrower than *monticola*, a trifle longer but more slender than the aedeagus.

Holotype, ♂, Gothic, 9,600 ft., along Copper Creek below Judd Falls, July 6, 1934 (Alexander). Paratopotype, ♂, August 2, 1934.

The nearest relative is *Rhabdomastix (Sacandaga) monticola* Alexander, which differs especially in the venation and in details of structure of the male hypopygium, as compared above. The normal species of the genus have the outer dististyle quite different in structure, with abundant spines and spicules scattered over the entire outer surface.

Rhabdomastix (Sacandaga) subfasciger Alexander, 1927.—Gothic, 9,500 ft., July 6, 1934; Kebler Pass, 10,000 ft., July 15, 1934. In the present species there is some variation in the length of vein R_4 , in cases this being subequal to the petiole of cell R_3 , in other specimens slightly exceeding this distance.

Rhabdomastix (Sacandaga) neolurida sp. nov. — Belongs to the *lurida* group; general coloration dark brown and yellow, the praescutum patterned with two more or less distinct intermediate dark stripes; pleura variegated with dark brown; fore femora chiefly blackened, the remaining femora obscure yellow with their distal ends narrowly blackened; wings subhyaline, the prearcular and costal portions slightly more yellow; R_3 relatively short, oblique; male hypopygium with the gonapophyses unusually elongate, gradually narrowed to the very long acute blackened points.

♂. Length, about 4.5-5 mm.; wing, 5.4-5.8 mm.; antenna, about 1.5-1.6 mm.

♀. Length, about 5.5-5.5 mm.; wing, 5.5-6 mm.

Rostrum obscure brownish yellow to yellow; palpi black. Antennae black throughout, relatively elongate in male, as shown by the measurements; flagellar segments passing through oval to elongate oval, the more basal segments with one face slightly more protuberant; segments clothed with a dense erect pale pubescence that is shorter than the diameter of the segment; verticils shorter than the segments, unilaterally distributed. Head gray; anterior vertex wide.

Pronotum light yellow, restrictedly darkened medially. Mesonotal praescutum almost uniform dark brown, sparsely pruinose, the humeral and lateral portions restrictedly more yellow; in cases, the praescutum with more or less distinct intermediate dark stripes; pseudosutural foveae large, reddish brown; scutum and scutellum chiefly dark brown, the posterior margin of latter, with the parascutella, paler; postnotum chiefly yellow, the posterior portion narrowly more darkened; in cases, the postnotum more uniformly blackened. Pleura obscure yellow, conspicuously patterned with dark brown on the anepisternum, ventral sternopleurite and meron. Halteres uniformly pale yellow. Legs with the coxae more or less infuscated, especially the fore pair; trochanters obscure yellow; fore femora chiefly blackened, the basal third obscure yellow; remaining femora yellow, the tips more narrowly blackened, narrowest on the posterior pair where about the outer seventh is included; fore tibiae and tarsi brownish black to black; middle and posterior tibiae and basitarsi obscure yellow, their tips blackened; remainder of tarsi black. Wings (Fig. 22) subhyaline, the prearcular and costal fields slightly more yellow; veins dark brown, those of basal and cephalic portions more yellow. Venation: Sc relatively long, Sc_1 ending a short distance before fork of the long Rs , Sc_2 atrophied; vein R_3 relatively short, oblique, the distance on costa between R_{1+2} and R_3 nearly equal in length to vein R_3 alone; $m-cu$ oblique, at near midlength of cell 1st M_2 . In cases, a vague trace of vein R_2 present, placed just before midlength of petiole of cell R_3 .

Abdominal segments black, the lateral borders very narrowly yellow; hypopygium brownish black. Male hypopygium (Fig. 29) with the outer dististyle, *od*, relatively narrow, the apical point stout. Gonapophyses, *g*, unusually long, gradually narrowed to very long acute blackened points.

Holotype, ♂, Arizona Creek, Grand Tetons National Forest, Wyoming, 6,700 ft., July 8, 1941 (Alexander). *Allotopotype*, ♀. *Paratopotypes*, numerous ♂ ♀.

In addition to the above described species, I am further differentiating a subspecies of the same.

Rhabdomastix (Sacandaga) neolurida setigera subsp. nov. — Compared with the typical subspecies, differs as follows: Antennae (male) even more elongate, the individual flagellar segments correspondingly longer; erect pale pubescence of segments longer and more conspicuous, exceeding in length the transverse diameter of a segment. Wings (Fig. 24) broader, with the veins medium brown, more uniform in color over the entire disk. Venation: Cells correspondingly wider, due to the increase in wing width; R_{2+3+4} only about one-third longer than R_3 , in the typical form nearly twice the length of this vein; R_3 even more longitudinal in position, in approximate alignment with R_{2+3+4} . Male hypopygium with the gonapophyses less elongate, especially the narrowed apical portion.

Holotype, ♂, Gothic, 9,500 ft., July 6, 1934 (Alexander). *Allotopotype*, ♀, with the type. *Paratopotypes*, several ♂ ♀, July 9-18, 1934.

The *lurida* group of *Rhabdomastix* is well-distinguished by the loss of vein Sc_2 and the pointed gonapophyses. To this date, members of the group were known only from Eurasia (*inclinata* Edwards, 1938; *lurida* Loew, 1873, of the western Palaearctic region; *luridoides* Alexander, 1940, of the eastern Palaearctic region). The present fly is closest to *luridoides*, differing especially in the coloration and details of structure of the male hypopygium. The two European species have the gonapophyses much shorter than in the other species though still pointed at their tips. The exact homologies of these latter structures still remain in question. Both Edwards (1938) and Alexander (1940) considered them as representing parameres (gonapophyses) but from their position I am not at all certain of this homology, it being at least possible that they are actually interbases.

Erioptera (Erioptera) septemtrionis Osten Sacken, 1859.—Gothic, slopes of Mount Avery, 10,000 ft., July 5, 1934 (Hallahan); Gothic Valley, on trail to Emerald Lake, 10,000 ft., July 12, 1934 (M. M. A.). *E. (E.) subseptemtrionis* Alexander, 1920, seems now not to be separable from typical *septemtrionis*.

Erioptera (Ilisia) hygropetrica sp. nov. — General coloration dull black, sparsely pruinose; antennae black throughout; halteres elongate, dark; wings

with a strong brown tinge, the stigmal region and anterior cord vaguely darkened; cell 1st M_2 closed, small; *m-cu* close to the fork of *M*; vein 2nd *A* nearly straight; male hypopygium with the mesal face of basistyle produced into a short arm that bears conspicuous blackened points; outer dististyle bifid, the inner arm with conspicuous slender teeth.

♂. Length, about 4.5-5 mm.; wing, 5.8-6.2 mm.

♀. Length, about 4.5 mm.; wing, 5 mm.

Rostrum dark gray; palpi black. Antennae black throughout; flagellar segments oval, with long outspreading verticils. Head black, sparsely dusted with gray.

Pronotum brownish black, the scutellum more reddish brown. Mesonotum dull black, the surface sparsely pruinose. Pleura black, sparsely pruinose. Halteres unusually long and slender for a member of this genus, stem dusky, knob even darker. Legs with the coxae and trochanters brownish black; remainder of legs brownish black, the terminal tarsal segments blackened; vestiture of legs relatively short and appressed. Wings (Fig. 23) broad, with a strong brownish tinge, the stigmal region and anterior cord vaguely seamed with darker; veins brown. Venation: Sc_1 ending opposite R_2 , Sc_2 about opposite one-fourth to one-third the length of *Rs*; cell 1st M_2 closed, small, less than one-half vein M_4 beyond it; *m-cu* close to the fork of *M*, in cases shortly beyond this fork; vein 2nd *A* nearly straight, cell 2nd *A* relatively narrow.

Abdomen, including hypopygium, black. Male hypopygium (Fig. 30) having the caudal margin of ninth tergite, *9t*, with a broad U-shaped notch, the adjoining lobes thus formed unusually slender. Basistyle, *b*, with mesal face at cephalic end produced into a short arm that bears conspicuous blackened denticles. Outer dististyle, *od*, bifid, blackened, the outer arm more slender, with appressed teeth on outer margin; inner arm shorter and broader, the margin with numerous slender teeth, their tips obtuse. Inner dististyle, *id*, shorter, pale, the narrowed tip bearing a single strong seta; face of style with a tubercle tipped with two even longer setae. Outer gonapophysis, *og*, appearing as a flattened pale blade, the tip obtuse. Inner gonapophysis, *ig*, appearing as slender, gently curved horns that subtend the short aedeagus, each gradually narrowed into a pale acute point.

Holotype, ♂, 9,500 ft., July 13, 1934 (Alexander). *Allotopotype*, ♀, July 29, 1934. (*M. M. Alexander*). *Paratopotypes*, 5 ♂♂, July 13-19, 1934 (Alexander). This very interesting crane-fly was found only along East River near the old saw-mill, under conditions described under the account of *Elliptera coloradensis* Alexander on a previous page. The flies were taken while resting in the dryer places on the vertical wooden wall where a film of water constantly trickled and flowed. Here it was associated with numerous other hygroptetic Diptera of several families, including the *Elliptera*. A single specimen of *Ormosia* (*Ormosia*) *hallahani* sp. nov. was also secured here.

Erioptera (*Ilisia*) *hygropetrica* is very different from all other described

American species of the genus. In its venation, it is closest to the various light yellow species that center about *microcellula* but it is entirely different in coloration and in the structure of the male hypopygium.

Erioptera (Ilisia) lucia Alexander, 1914.—Gothic, 9,500-10,100 ft., July 9-12, 1934. Other records: Estes Park, Colorado, August 10, 1919 (*Claassen*); Webster, Colorado, August 24, 1915 (*E. J. Oslar*).

Erioptera (Ilisia) margarita Alexander, 1919.—Gothic, 9,500 ft., July 2-11, 1934. Other record: Colorado Springs, Colorado, June 8, 1915 (*M. C. VanDuzee*).

Erioptera (Ilisia) microcellula Alexander, 1914.—Above Gothic, 10,100 ft., July 12, 1934; along a small clear mountain stream, common.

Erioptera (Psiloconopa) aperta (Coquillett, 1905) (*mormon* Alexander, 1927).—Gothic, 9,500 ft., July 2-6, 1934. A common and wide-spread species throughout the central and northern Rockies. The distinctions used to separate the subgeneric groups *Psiloconopa* Zetterstedt, 1838, and *Ilisia* Rondani, 1856, are becoming more difficult to maintain as new species are constantly being discovered.

Erioptera (Psiloconopa) gaspicola (Alexander, 1929).—Gothic, 9,500 ft., July 19, 1934. Hitherto known only from the Gaspé Peninsula, eastern Quebec.

Erioptera (Helobia) cana (Walker, 1848).—Gothic, 9,500 ft., July 4-12, 1934.

Erioptera (Mesocyphona) splendida (Alexander, 1913).—Gothic, 9,500-10,100 ft., July 4-12, 1934.

Erioptera (Empeda) cinereipleura (Alexander, 1917).—Gothic, 9,500 ft., July 4, 1934.

Ormosia (Ormosia) megarhabda sp. nov. — General coloration brownish gray, the praescutum with a conspicuous, darker brown, median stripe; antennae black throughout; halteres yellow; leg dark brown to brownish black; wings with a faint yellowish tinge, unpatterned; macrotrichia of cells long but sparse; cell M_2 open by atrophy of m ; vein 2nd A elongate, subsinuous; male hypopygium with the dististyles apical in position, outer style profoundly bifid, both arms microscopically spiculose; inner dististyle gently arcuated; gonapophyses appearing as very powerful blackened horns.

♂. Length, about 4.5-5 mm.; wing, 5-6 mm.

♀. Length, about 5.5 mm.; wing, 5.5 mm.

Rostrum brownish black; palpi dark brown. Antennae black throughout; flagellar segments oval, those of more than the outer half with segments more slender and attenuated; verticils very long and conspicuous, especially on the more proximal segments. Head dark brown.

Pronotum brownish gray; pretergites conspicuously light yellow. Mesonotum brownish gray, the praescutum with a conspicuous, darker brown, median stripe, the lateral stripes not or but poorly differentiated; scutellum more yellowish brown to obscure yellow. Pleura brownish gray; dorso-pleural region slightly paler. Halteres yellow throughout. Legs with coxae brownish gray; trochanters brownish yellow; remainder of legs dark brown to brownish black. Wings (Fig. 31) with a faint and uniform yellowish tinge, without pattern; veins brown. Cells of wing with sparse but conspicuous, elongate setae, distributed over the entire wing surface; macrotrichia of veins only a trifle longer and stouter. Venation: Sc_1 ending about opposite R_2 , Sc_2 at near midlength of R ; cell M_2 open by atrophy of m ; vein 2nd A elongate, feebly sinuous to nearly straight, about intermediate in condition between strongly arcuated to straight.

Abdomen dark brown, the hypopygium slightly brightened. Male hypopygium (Fig. 36) with the basistyle, b , simple, at apex produced into a short conical lobe. Outer dististyle, od , profoundly bifid on outer half, both arms microscopically spiculate, one arm much stouter than the other. Inner dististyle, id , a long slender gently arcuated pale blade. Gonapophyses, g , appearing as very powerful blackened simple horns on either side of the very small aedeagus.

Holotype, ♂, 9,500 ft., July 4, 1934 (Alexander). *Allotopotype*, ♀, pinned with type. *Paratopotypes*, numerous ♂ ♀, July 7-19, 1934 (Alexander).

Ormosia (Ormosia) megarhabda is very distinct from the other Nearctic species of the genus so far described. The venation is almost identical with that of the genus *Erioptera* but from the presence of sparse but conspicuous trichia over the entire wing surface, it seems that the fly is better assigned to *Ormosia*. The structure of the male hypopygium, especially of the gonapophyses, is very different from that of other members of the genus.

Ormosia (Ormosia) hallahani sp. nov. — General coloration black, the mesonotum only sparsely pruinose so that the surface appears subnitidous; head and thoracic pleura heavily gray pruinose; halteres pale yellow; femora yellow, the tips narrowly but conspicuously blackened; wings whitish subhyaline, the stigma conspicuous, dark brown; a brown seam along vein Cu , with more restricted markings along cord and as a delicate border to the wing; cell 1st M_2 closed; anal veins divergent; male hypopygium with the basistyle profoundly notched, to produce a ventral and a dorsal lobe, the dististyles arising from this notch; inner dististyle slender, especially the distal half which appears as a long straight spine.

♂. Length, about 5 mm.; wing, 5.8-6 mm.

Rostrum and palpi black. Antennae black throughout; flagellar segments oval, the verticils shorter than the segments. Head black, heavily pruinose.

Pronotum dark brown, the pretergites conspicuously light yellow, the marking continued caudad to the wing-root. Mesonotal praescutum black, the surface very sparsely pruinose so the general appearance is subnitidous; posterior callosities of scutal lobes more reddish brown. Pleura black, heavily gray pruinose. Halteres pale yellow. Legs with the coxae pale brown; trochanters yellow; femora yellow, the tips narrowly but conspicuously blackened, the amount subequal on all legs; tibiae and basitarsi obscure yellow, the tips narrowly blackened, remainder of tarsi black. Wings (Fig. 32) whitish subhyaline, patterned with dark brown, including an unusually conspicuous stigmal area; a conspicuous brown seam along vein *Cu* and narrower darkenings along cord and as a delicate border from vein *R*₃ continued entirely around the wing to

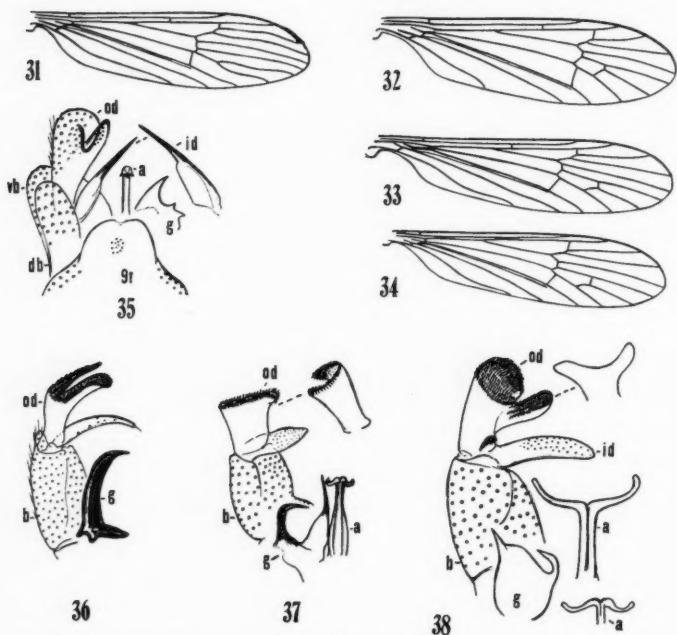


Fig. 31. *Ormosia (Ormosia) megarhabda* sp. n.; venation.
 Fig. 32. *Ormosia (Ormosia) hallahani* sp. n.; venation.
 Fig. 33. *Ormosia (Ormosia) libella* sp. n.; venation.
 Fig. 34. *Ormosia (Ormosia) suffumata* sp. n.; venation.
 Fig. 35. *Ormosia (Ormosia) hallahani* sp. n.; male hypopygium.
 Fig. 36. *Ormosia (Ormosia) megarhabda* sp. n.; male hypopygium.
 Fig. 37. *Ormosia (Ormosia) libella* sp. n.; male hypopygium.
 Fig. 38. *Ormosia (Ormosia) suffumata* sp. n.; male hypopygium.
 (Symbols: a, aedeagus; b, basistyle; db, dorsal lobe of basistyle; g, gonapophysis; id, inner dististyle; od, outer dististyle; t, tergite; vb, ventral lobe of basistyle.)

vein 2nd *A*; veins brown, more yellow in prearcular field and at base of *Sc*. Trichia of cells abundant, more sparse or lacking in bases of cells *Cu*, 1st *A* and 2nd *A*. Venation: *Sc*₂ nearly opposite midlength of *Rs*; cell 1st *M*₂ closed; *m-cu* about one-third to one-fourth its own length beyond fork of *M*; anal veins divergent.

Abdomen black, sparsely pruinose; hypopygium black. Male hypopygium (Fig. 35) with the extensive median lobe of tergite, 9*t*, broadly depressed, weakly bilobed at apex. Basistyle, *b*, deeply bilobed into a ventral, *vb*, and a dorsal, *db*, lobe, with the two dististyles arising from this notch. Outer dististyle, *od*, very large and massive, unequally bilobed, the major outer lobe very large and massive. Inner dististyle, *id*, slender, the basal half stouter, the distal half narrowed into a long slender spine. Gonapophyses, *g*, appearing as flattened spinous blades. Aedeagus slender, straight, terminating in a small bell-shaped cap.

Holotype, ♂, Gothic, 9,500 ft., July 13, 1934 (Alexander). Associated with *Elliptera coloradensis* Alexander and *Erioptera (Ilisia) hygropetrica* sp. nov., as discussed earlier in the present report.

Ormosia (Ormosia) hallahani is named in honor of Mr. John D. Hallahan, to whom I am greatly indebted for numerous specimens of Tipulidae from the Gothic Area. The species is quite distinct from certain other approximately similar regional species, as *O. (O.) fumata* (Doane, 1900) and *O. (O.) bifidaria* Alexander, 1919, being more closely related to a group of species hitherto believed to be restricted to the eastern Palaearctic region, including *O. (O.) cata* Alexander, 1940, *O. (O.) deprava* Alexander, 1941, and *O. (O.) prava* Alexander, 1940, all of Japan and northern Korea.

Ormosia (Ormosia) bifidaria Alexander, 1919.—Gothic, 9,500 ft., July 2, 1934; trail to Emerald Lake, 10,100 ft., along a small mountain stream.

Ormosia (Ormosia) libella sp. nov. — Belongs to the *fumata* group; mesonotal praescutum gray, with three brown stripes; femora and tibiae obscure yellow, their tips weakly darkened; wings whitish subhyaline, stigma brown; anal veins convergent, 2nd *A* strongly sinuous; male hypopygium with the outer dististyle only weakly expanded outwardly, the apex scarcely emarginate, provided with abundant blackened spinous points; gonapophyses with the outer spines relatively slender, strongly curved, the inner spine long and nearly straight; apical arms of aedeagus unusually short and relatively inconspicuous.

♂. Length, about 5.5-6 mm.; wing, 6.65 mm.; antenna, about 1.5 mm.

Rostrum brownish gray; palpi dark brown. Antennae of moderate length, brownish black throughout; flagellar segments passing through long-oval to elongate; longest verticils slightly exceeding the segments. Head dark gray.

Pronotum brownish gray; pretergites conspicuously yellow. Mesonotal praescutum gray with three brown stripes, the median one especially broad and

conspicuous; pseudosutural foveae black; scutum gray, each lobe with two poorly marked brown areas; posterior portion of scutal lobes and the scutellum obscure orange, parascutella dark; postnotum gray. Pleura gray. Halteres pale yellow throughout. Legs with the fore coxae brownish gray, middle and posterior coxae more yellowish; trochanters yellow; femora and tibiae obscure yellow, the tips weakly darkened; tarsi dark brown. Wings (Fig. 33) whitish subhyaline to weakly tinged with brown; stigma brown; a poorly indicated darkening on anterior cord; veins brown, those in prearcular field more yellow. Macrotrichia of cells numerous and well-distributed. Venation: R_{2+3} subequal to R_2 alone; vein 2nd *A* strongly sinuous.

Abdominal tergites brownish gray, basal sternites somewhat brightened; subterminal segments more uniformly dark brown; hypopygium yellow, the basistyles weakly darkened. Male hypopygium (Fig. 37) with the outer dististyle, *od*, pale, darkened apically, the outer portion weakly expanded but scarcely emarginate, the margin provided with very abundant blackened spinous points. Inner dististyle flattened, narrowed to the subobtusate apex. Gonapophyses, *g*, with the outer spine relatively slender, curved more or less strongly to a long straight point; inner spine long and nearly straight, subtending the aedeagus. Aedeagus, *a*, with the apical arms unusually short and relatively inconspicuous.

Holotype, ♂, Gothic, 10,100 ft., July 12, 1934, along small mountain stream. (*Alexander*). *Paratopotypes*, 2 ♂♂; *paratypes*, 9,500 ft., 2 ♂♂, July 3, 1934; 1 ♂, July 18, 1934.

Ormosia (Ormosia) libella is readily told from the other species that are allied to *fumata* (Doane) by the structure of the male hypopygium. The short apical arms of the aedeagus are more as in *O. (O.) garretti* Alexander, 1926, than in *O. (O.) bifidaria* Alexander, 1919; *O. (O.) fumata* (Doane, 1900) or *O. (O.) suffumata* sp. nov.

Ormosia (Ormosia) suffumata sp. nov. — Belongs to the *fumata* group; general coloration of thorax yellow, the dorsum patterned with brownish gray, including four virtually confluent praescutal stripes; pleura not or but feebly darkened; halteres uniformly pale yellow; wings with a weak brown tinge, the prearcular and costal fields more yellow; stigma and a restricted seam along cord darker brown; vein 2nd *A* strongly sinuous; male hypopygium with the outer dististyle conspicuously dilated at apex; gonapophyses appearing as flattened blades, each bearing two unequal spines; apical lobes of aedeagus long and gently sinuous.

♂. Length, about 5.3-5.5 mm.; wing, 6-6.2 mm.

Rostrum obscure yellow; palpi brown. Antennae with the basal three segments yellow, the succeeding ones passing into brown; flagellar segments oval to long-oval. Head uniformly gray.

Pronotum brownish gray, obscure yellow medially behind. Mesonotal

praescutum with the humeral and lateral portions yellow, the disk chiefly covered by four more brownish gray stripes that are virtually confluent, obliterating the posterior interspaces or nearly so; tuberculate pits black, conspicuous, pseudosutural foveae more reddish brown; scutal lobes brownish gray, the median area paler; scutellum obscure yellow; postnotum brownish gray. Pleura variegated yellow and pale brownish gray, the latter color sometimes lacking, in other cases involving the mesepisternum and meron. Halteres pale yellow. Legs with the coxae and trochanters yellow; femora obscure yellow, the tips not or scarcely darkened; tibiae and basitarsi yellow, their tips pale brown; remainder of tarsi black. Wings (Fig. 34) with a weak brown tinge, the prearcular and costal fields more yellow; stigma and a restricted seam along cord darker brown; veins brown, paler in the flavous areas. Macrotrichia of cells abundant and distributed over the entire wing excepting the extreme basal portions of cell Cu. Venation: Vein 2nd A strongly sinuous, on distal third or more paralleling the posterior margin of wing. In one wing of a paratype, *m* is atrophied so that cell *M*₂ is open.

Abdominal tergites dark grayish brown, the sternites and outer two segments yellow. Male hypopygium (Fig. 38) as in the *fumata* group. Outer dististyle, *od*, widely dilated apically, with rows of abundant blackened setae or short spines. Gonapophyses, *g*, appearing as flattened blades, the mesal portion of each produced into a long curved spine, the outer angle into a shorter acute spinous point. Apical lobes of aedeagus, *a*, long and gently sinuous.

Holotype, ♂, Peaceful Valley, Boulder Co., Colorado, August 25, 1918 (T. D. A. Cockerell). *Paratopotypes*, 3 ♂♂, August 25, 1918; August 1919 (T. D. A. Cockerell).

Although the present species has not been taken in the Gothic Area it is included herewith in order to add to the data regarding the *fumata* group. The fly has long been confused in my collection with *Ormosia* (*Ormosia*) *fumata* (Doane, 1900), of the north-central Rocky Mountain region, which is now known to differ in coloration and in the structure of the male hypopygium. I am greatly indebted to Dr. Alan Stone, of the United States National Museum for mounting the male hypopygium of the type of *fumata*; this shows the details of the hypopygium, especially the gonapophyses, to be quite distinct from those of the present fly.

Ormosia (*Ormosia*) *cockerelli* (Coquillett, 1901).—Gothic, 9,800-10,100 ft., July 3-12, 1934.

A Taxonomic Distinction Between *Cyllene robiniae* (Forst.) and *Cyllene caryae* Gahan

Edwin W. King*

Considerable difficulty is usually encountered in distinguishing between the two common Cerambycid beetles, *Cyllene robiniae* (Forster) and *Cyllene caryae* Gahan, commonly known as the locust borer and the painted hickory borer, respectively. Biologically, the two species are quite distinct: *C. caryae* breeds in hickory and emerges in the spring; *C. robiniae* breeds in locust and emerges in the late summer. Morphologically, however, there are few, if any, characters which, without reference to a data label, will serve positively to determine an isolated specimen.

In this study, a close examination was made of a number of hind wings of both species. The *robiniae* series used consisted of 28 wings; the *caryae* series, of 11. Characters observed may be grouped broadly into three categories: those of coloration, venation,** and chaetotaxy.

Pigmentation, as considered here, may be arbitrarily divided into (a) ground color, and (b) pattern. The former may be defined as the diffused pigment which, to a greater or lesser extent, covers the entire wing. Pattern, on the other hand, is the darker, more sharply defined areas of pigment superimposed upon the ground color.

Differences in coloration of the wings of the two species are so well-marked in each member of the two series as to make the following characterization apparently true:

Brown pigment of ground color extending uniformly over the wing as far basad as 2nd A_3 + 3rd A_1 ; i.e. the entire discal cell and the vannus transparent only in small triangles at their bases. Over nearly their whole area, these cells a uniform chestnut-brown. *Cyllene robiniae*

Brown pigment of ground color light brown or lacking entirely in the discal cell and in the vannus; if present, not extending over the whole area included in these fields; i.e. the posterior half of the discal cell and the basal half of the vannus nearly transparent. *Cyllene caryae*

It also appears that the pattern in the area of the radial cell differs with the two species, and this difference may also aid in distinguishing between them. In the wing of *C. caryae* the pattern of this region is nearly black, the density of pigment being the more noticeable because of the relative transparency of the distal end of the discal cell. In the wing of *C. robiniae* the pattern of the radial cell region is dark brown, but the pattern is not so sharply contrasted with the surrounding ground color which, as already observed, is

* The writer is indebted to Dr. R. N. Jefferson, of the Virginia Agricultural Experiment Station, for several specimens of *C. caryae*.

** Venation according to Forbes, Ann. Ent. Soc. Am. 5:15, 1922, pp. 328-352.

darker in the discal cell than is the corresponding part of the wing of *C. caryae*.

In the region of the tip of the wing, distal to the radial cell and $M_4 + Cu$, *C. caryae* shows a rather sharp change in the density of pigment, the line of demarcation being the Vein M_1 . Anterior to vein M_1 , color is considerably darker than it is posterior to that vein. Such a change does not occur in *C. robiniae*; ground color density in cell M_1 does not differ from that of the area immediately anterior to it.

No satisfactory means of separation of the two species on the basis of

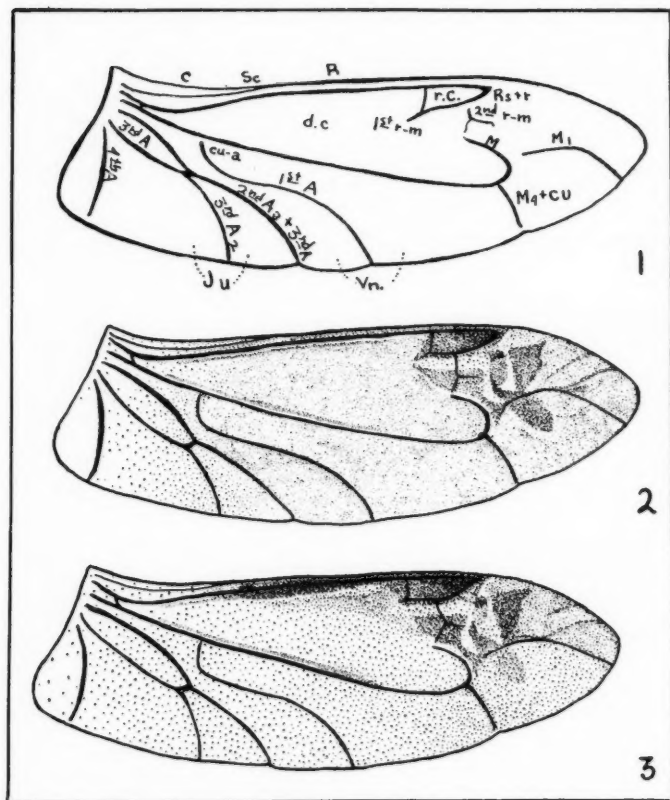


Fig. 1. Diagram of typical wing; dc, discal cell; Ju, jugum; rc, radial cell; Vn, vannus. Fig. 2. *Cyllene robiniae*. Fig. 3. *Cyllene caryae*.

venation was discovered. The venation was quite similar and remarkably constant in all specimens observed.

Setae on the two wings are confined to the center of the triple fork junction of M and $M_4 + Cu$. From 2 to 7 setae were observed in this fork, their arrangement and number varying so much as to render them useless as taxonomic characters.

The wings are uniformly pubescent, but no differences could be observed after examination of this character.

SUMMARY

Observations were made upon a series of 11 and 28 wings of *Cyllene caryae* Gahan and *Cyllene robiniae* (Forst.), respectively.

A method of distinguishing between the two species on the basis of wing coloration is described.

An examination of wing venation, pubescence, and chaetotaxy yielded no distinction between the two species.

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A New Subspecies of *Formica moki* Wheeler (Hymenoptera: Formicidae)¹

A. C. Cole, Jr.

In 1939, Smith² described a new subspecies of *Formica moki* Wheeler, which he named *xerophila*. In the same paper he also redescribed the worker of *moki* as follows:

Worker—Length 4-5.5 mm.

Head, exclusive of mandibles, one-seventh to one-ninth longer than broad, narrower in front than behind, with entire and gently rounded posterior border, rounded posterior angles, and weakly convex sides. Eye large, convex, oblong, little more than its greatest diameter from base of mandible. Antenna long and slender, scape approximately as long as the combined lengths of the first 7 or 8 funicular segments; middle funicular segments about twice as long as wide. Clypeus sharply carinate, anterior border entire, projecting medianly. Frontal and ocellar triangles almost equilateral. Frontal carinae slightly diverging behind. A faint frontal furrow often extending as far backward as anterior ocellus. Mandible 7- or 8-toothed. Maxillary palpus long, slender, 6-segmented. Thorax long, narrow; mesoepinotal constriction shallow; base and declivity of epinotum subequal, the base sloping to meet the declivity in an obtuse angle. Pronotum viewed from above almost as long as broad; mesonotum approximately one and a half times as long as broad. Petiole with a moderately convex anterior surface, and flat posterior surface, the two meeting above to form a sharp, straight or sometimes feebly rounded superior border. Gaster small. Legs long and slender.

Subopaque, finely and densely shagreened; mandibles, sides of clypeus, and frontal area slightly shining in certain lights. Mandibles densely striate, and also coarsely punctate. Posterior dorsal surface of head and the gaster with a metallic or bronzy luster in certain lights.

Hairs grayish, sparse, erect, present on clypeus, dorsal surface of head, coxa, trochanter, and flexor surfaces of femora and tibiae, and on gaster; hairs on mandibles suberect; hairs on gaster shorter than on venter and at apex. Pubescence grayish, fine and dense, covering all parts of body, but densest on gaster.

Dull ferruginous; dorsal surface of head posteriorly, and the petiole, gaster, and legs dark brown; in some lights parts of the thorax may have a brownish or infuscated cast.

The type locality of *moki* is Bright Angel Trail, Grand Canyon, Arizona, 5,500-7,000 feet. Other localities from which the species has been recorded are Prescott, Arizona, and Milford, Blanding and Bluff, Utah. I have a small series of what I consider to be *moki* collected in Millard Co., Utah, by D. M. Rees. These specimens have very distinct splotches of brown on the thoracic dorsum.

¹ Contribution No. 6, Department of Zoology and Entomology, University of Tennessee, Knoxville.

² Smith, M. R. Notes on *Formica* (Neofornica) *moki* Wheeler, with description of a new subspecies, *Ann. Ent. Soc. Amer.* 32:581-584, 1939.

Smith³ described his subspecies *xerophila* as follows:

Worker.—Length 5.3-5.6 mm.

Similar to *moki* except for the following differences: mandibles uniformly 8-toothed in all specimens examined; petiole thicker antero-posteriorly, and with blunter, more rounded, and feebly notched superior border; pubescence of body apparently denser, therefore more distinct; general color blackish with anterior part of head, and the antennae, tibiae, and tarsi reddish brown; body, especially the posterior dorsal portion of head, and the gaster, with a metallic luster in certain lights.

Type locality.—Leavenworth, Wash. (Falconer Smith).

***Formica moki* subsp. *grundmanni* nov.**

Worker.—Length, 5.5-6.5 mm. (Cole collection No. U-36).

Differs from *moki* in the following respects: Greater body length; mandibles uniformly 8-toothed in all specimens examined; mesoepinotal constriction somewhat deeper; thorax more robust; petiole very much thicker anterioposteriorly, with an extremely convex anterior surface, superior border very blunt, more rounded and feebly but distinctly excised; pubescence denser and hence more obvious, especially on posterior dorsal portion of head and on gaster; legs, especially the femora and tibiae, reddish brown; indistinct splotches of brown on pronotum and mesonotum; gaster much darker than legs in many specimens, in some specimens nearly black.

Differs from *moki* subsp. *xerophila* as follows: Thorax shorter and stouter; petiole thicker anterioposteriorly, with a more blunt superior border; pubescence denser; body surface less shagreened; color of body lighter.

The specimens upon which this description is based were collected in soil beneath stones in Parleys Canyon, Salt Lake Co., Utah, by A. W. Grundmann. The type series consists of 30 workers. Cotypes are to be deposited in the U. S. National Museum, the American Museum of Natural History and the Department of Zoology of the University of Utah.

The writer is much indebted to Dr. M. R. Smith, at the U. S. National Museum, who kindly compared specimens of *grundmanni* with types of *xerophila*.

³ *Op. cit.*, p. 583

Known Distribution of the Shining Slave Maker Ant *Polyergus lucidus* Mayr

Joseph W. Jones, Jr.

In view of recent collection records from the Southern States the writer has deemed it worthwhile to report the occurrence of the Shining Slave-maker Ant, *Polyergus lucidus* Mayr from this region. While this ant species is apparently not uncommon in the Northeastern States it is also found occasionally to the south and west, although not as a commonly established species. Of the four instances reported by this writer, it is interesting to note that the colony nearest the center of dispersal was the strongest and largest of each group and that the weaker colonies were successively further south and west. Moreover, the most southern record produced only two workers which were found wandering along one of the main line railroads. In this instance a formicary could not be located although a thorough search was made of the adjacent area, since it was expected the colony must be close by. This may well be a case of incidental occurrence since these specimens could easily have been brought in from elsewhere.

Specimens were determined by Dr. A. C. Cole, Jr. of the University of Tennessee and by Dr. M. R. Smith of the United States National Museum.

Dr. M. R. Smith, through the Division of Insect Identification of the Bureau of Entomology and Plant Quarantine, has kindly furnished the locality records of this ant other than those reported by the writer.

Locality records are as follows:

Colorado: Colorado Springs (W. M. Wheeler). Connecticut: (Listed from state by Gustav Mayr). Indiana: Pine, W. S. Blatchley. Kentucky: Lexington (H. H. Jewett). Massachusetts: Falmouth, West Falmouth (A. H. Sturtevant). Mississippi: Abbeville (two workers taken by J. W. Jones, Jr.). New Jersey: Camden County (J. B. Smith); Clementon (Fox); Vineland (Mrs. Treat). New York: White Plains, W. Nyack (Joseph Bequaert); Bronxville (W. M. Wheeler); Pine Lawn and Selden, Long Island (Wm. T. Davis collection). North Carolina: Belmont (P. J. Schmitt); Conover (H. T. Vanderford). Ohio: South central (L. G. Wesson, Jr.). Pennsylvania: Rebersburg (L. E. Shinn). South Carolina: Whitewater Falls, Florence (M. R. Smith). Tennessee: Bluff City, Ringgold (J. W. Jones, Jr.). Virginia: Bristol (J. W. Jones, Jr.).

Polyergus lucidus was described by Mayr (Verh. Zool.-Bot. Gesell. Wien 20:952, 1870) from specimens taken by Norton in Connecticut.

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Limnological Variables in a Colorado Mountain Stream¹

Robert W. Pennak

During the past forty years a great deal of limnological research has been carried out on all types of bodies of standing water, from large lakes and reservoirs to small ponds and bogs. Although some extensive work has also been done on lotic environments (see especially the papers of Allen, Behning, Galtsoff, Kofoid, Reinhard, and Richardson), it is generally agreed that our knowledge of streams and rivers lags far behind. Little specific information is available concerning the chemistry, physics, and biology of small, rapid streams. Mountain streams have been especially neglected, and although thousands of miles of high-altitude streams have been "surveyed" by various state and federal agencies, the great bulk of this information deals chiefly with bottom fauna productivity and the nature of the stream bed with reference to stream improvement work and the formulation of stocking policies. Many of these observations are accompanied by other biological data, but in the majority of instances such data are incidental and not readily available. Similarly, taxonomic studies on mountain stream fauna and flora usually contain little ecological information. Aside from such investigations, however, there are perhaps thirty or forty significant papers dealing with mountain streams. Of these, the publications of Steinmann (1907), Thienemann (1912), and Muttkowski (1929) are probably the most comprehensive.

With the above facts in mind, the writer undertook a preliminary, year-round investigation of Boulder Creek, Colorado, a typical mountain stream.² The purpose of the present paper is to emphasize the variability of certain chemical, physical, and biological characteristics of this stream. All observations and collections were made at a station situated near the western edge of the city of Boulder at the base of the foothills.

Description of Boulder Creek

Middle and North Boulder creeks originate as several small tributary streams in the alpine and montane limnological zones in northern Colorado (Pennak, 1941). They flow eastward, join in the foothills zone, and then continue as Boulder Creek through the city of Boulder. In the plains zone about five kilometers east of Boulder the main stream is joined by South Boulder Creek. Middle and North Boulder creeks together drain about 350

¹ Contribution No. 4, Limnological Laboratory, Biology Department, University of Colorado.

² This investigation has been aided by grants from the Penrose Fund of the American Philosophical Society and the University of Colorado Graduate School Research Fund.

sq. km. of foothills and mountainous regions. Geologically, most of this drainage area is composed of relatively insoluble pre-Cambrian granites, gneisses, schists, and syenites.

In a straight line, the sampling station lies about 30 km. east of the headwaters of the stream, but the length of the main channels between these points is about 42 km. In this distance the elevation drops from 3600 to 1630 m. As might be expected, therefore, Boulder Creek and its tributaries are typical, swift, cascading mountain streams. In some places there is no true stream bed, the water simply flowing between boulders ranging up to two meters in diameter. For the most part, however, the stream bed is composed of coarse gravel, pebbles, and rocks up to 30 cm. in diameter. In the lower portion of the foothills zone as much as 30 per cent of the bed may be composed of sand. At the sampling station (Fig. 1) the stream bed is about 12 m. wide; this is one



Fig. 1. Boulder Creek sampling station at Boulder, Colorado, during low water in November, 1940.

of the widest places along the entire length of the stream, the average width being only two to five meters. As will be shown below, the flow of Boulder Creek varies greatly, depending mostly on the distribution and intensity of rains and melting snows. Except at high water, there are few pools which are more than one meter deep; on the other hand, however, the stream bed never becomes dry. Middle Boulder Creek is dammed to form Barker Reservoir about 27 km. above the sampling station. Water from this reservoir is bypassed through a conduit to a hydroelectric station which is situated at the side of the stream 20 km. below the dam and 7 km. below the confluence of the two main branches of the stream. At this power station the by-passed water flows back into the stream bed. At intervals some water is drawn off through two irrigation ditches west of the city of Boulder. In general, Boulder Creek is clear, but it becomes turbid during high water. Except for rare instances, when small quantities of mine wastes are emptied into the stream, there is no pollution.

The bottom fauna is of the same general type found in trout streams everywhere; productivity is relatively low. There is no true bottom flora although the rocks and pebbles are covered with a growth of diatoms and *Ulothrix*, especially in the foothills zone. The stream is frequently stocked with trout, but it is visited by so many fishermen that fishing is generally poor.

As pointed out by Welch (1935), it is difficult to classify lotic environments using ecological criteria because of the integrations of types. Some of the proposed classifications are simple and generalized (Carpenter, 1928); others are complex and detailed (Ricker, 1934). Most schemes, however, are based largely on stream flow. According to the classifications of Muttkowski (1929), Ricker (*op. cit.*), Carpenter (*op. cit.*), and Pearse (1939), Boulder Creek may be referred to as a cascading stream, swift soft-water trout stream, trout beck, and brook, respectively, at the sampling station.

Methods

Observations were made at intervals of seven to fifteen days between November 4, 1939, and January 18, 1941. Customarily, all measurements and samples were taken between 10 A. M. and 2 P. M. In all, thirty series of observations were made.

Stream Flow was measured using the formula of Embody (1927). Temperatures were taken 10 cm. below the surface with a tested laboratory thermometer. Hydrogen ion concentrations were determined with a Hellige disc comparator, using bromthymol blue and phenol red as indicators. The unmodified Winkler method was used for dissolved oxygen. Free and bound carbon dioxide were determined with N/44 sodium carbonate and phenolphthalein, and N/44 hydrochloric acid and methyl orange, respectively. While both of these methods may sometimes be unreliable because of the personal error in reading endpoints, all determinations in this investigation were precisely made by the same individual, and are believed to be relatively accurate. Total residues were determined by evaporating three liters of water to dryness at 60° C.; the organic content was taken as being equivalent to the loss on ignition at 600° C.

A ten-liter plankton trap was used for collecting the zooplankton organisms. Since it was equipped with No. 25 bolting silk, it is likely that very few zooplankters were lost during sampling. The organisms concentrated from the ten-liter water samples were preserved in 70 per cent alcohol. Qualitative and quantitative determinations were made by counting and identifying all of the organisms in each sample instead of using aliquot portions.

The phytoplankters were collected quantitatively by adding 30 cc. of formalin to one-liter water samples and allowing to stand for a week or ten days in graduated cylinders. At the end of that period most of the supernatant water was carefully siphoned off, and the residues containing the phytoplankton organisms were preserved in small vials. Counts were made with a Sedgwick-Rafter cell.

Physical and Chemical Conditions

Although the headwaters of Boulder Creek have temperatures below 5.0° C. during most of the year, such temperatures occurred only from November through March at the sampling station at the base of the foothills. The lowest temperature found was 0.4° on February 10, 1940; the highest was 20.6° on August 31, 1940. The average annual stream temperature in 1940 was 8.8° . This is exactly the same as the annual average temperature of the Mississippi River in 1928 (calculated from data given by Reinhard, 1931); it is considerably lower than the average of 14.2° for the Illinois River in 1898 (calculated from data given by Kofoed 1908). The daily fluctuations in water temperature were not determined although they were probably comparable with the values of 0.9° and 5.3° which Ricker (1934) found in the Mad River, Ontario, during the winter and summer, respectively.

Most mountain streams are characterized by great variations in flow, and Boulder Creek is no exception. During the present investigation the flow ranged from a trickle of only 0.9 cubic feet per second on October 13, 1940, to a torrent of 333.0 cubic feet per second on July 3, 1940 (latter figure not indicated in Fig. 2). In general, the stream was lowest during the fall and winter, and highest during the spring and early summer. There are several factors which produce great daily and seasonal variations in flow. First, the melting snows of the montane and alpine zones are responsible for generally persistent large stream flows during the spring and early summer. Second, the lighter snows of the foothills melt early in the spring and may sometimes cause freshets during unusually warm weather. Third, occasionally in the fall the thawing of an early snow in the foothills may also cause a large increase in the stream flow. The determinations of 64 and 82 cubic feet per second in November, 1939, (Fig. 2) were due to such thaws. Fourth, daily mountain showers are of considerable significance; these showers are usually brief and localized, although sometimes they are more general and approach cloudburst proportions. Since there is a rapid run-off in the hills and mountains, Boulder Creek has great daily variations in flow during the warmer months depending on the frequency, intensity, and distribution of precipitation. Typical spring freshets most frequently result from the addition of much rainwater to the high water already produced by melting snows.

At the base of the montane zone all of the water of Middle Boulder Creek flows into Barker Reservoir. The quantity of water by-passed from there to the hydroelectric station farther downstream is relatively constant, but there is an overflow from the dam only during a few months of the year, particularly in the early summer. The fluctuations of Boulder Creek at the sampling station, therefore, are mostly due to melting and precipitation along the entire length of North Boulder Creek, the foothills portion of Middle Boulder Creek, as well as the main stream between the confluence of its two main branches and the sampling station.

During the spring, summer, and fall water was drawn off at intervals into two irrigation ditches about five kilometers above the sampling station. Custo-

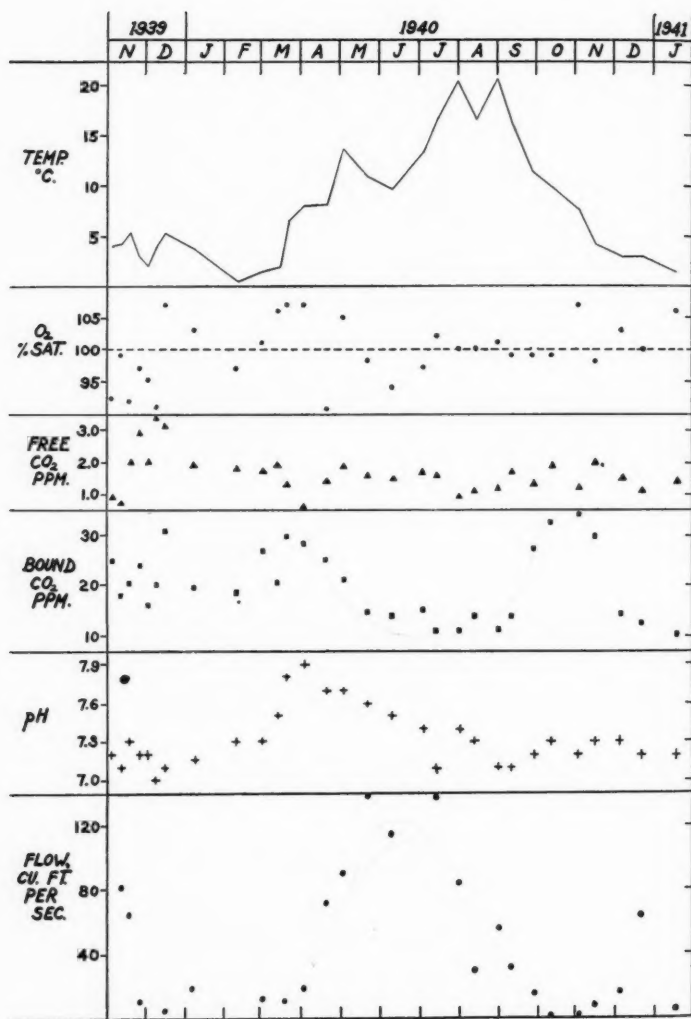


Fig. 2. Some chemical and physical characteristics of Boulder Creek at Boulder, Colorado.

marily, this diversion represented only a minor portion of the total flow, but during exceptionally low water it resulted in stream flow determinations of less than ten cubic feet per second.

Turbidity measurements were not made, but there was usually an obvious relationship between the height of the stream and the amount of silt in suspension. When the flow was less than ten cubic feet per second the presence of suspended silt could not be detected with the eye. In some instances, however, showers in the vicinity of Boulder caused much silting in spite of the fact that the stream flow was only 20 to 30 cubic feet per second.

The waters of Boulder Creek were always slightly alkaline, the range being pH 7.0 to 7.9. Out of a total of 30 determinations, five were pH 7.1, eight were 7.2, and seven were 7.3. Although the data shown in Fig. 2 indicate rather pronounced alkaline conditions during March, April, and May of 1940, these random samples are probably insufficient to warrant the conclusion that this was a definite spring trend. Certainly these more alkaline conditions did not appear to be correlated with any other limnological features of the stream.

In a shallow cascading mountain stream such as Boulder Creek, respiration and the decomposition of small amounts of organic matter have no appreciable effect on the amount of free carbon dioxide in solution. In fact, the constant agitation of the water serves to prevent the solution of all but a small amount. During the present investigation the free carbon dioxide content ranged from 0.7 to 3.5 p.p.m., although the great majority of determinations were between 1.0 and 2.0 p.p.m., and the average was 1.6 p.p.m.

The amounts of bound carbon dioxide, on the other hand, showed a comparatively great variation, from 11.0 to 34.2 p.p.m. It is generally accepted that there is a correlation between the bound carbon dioxide content and stream flow, the theory being that during rains or rapid melting of snows, the water quickly passes over the surface of the ground in rivulets and consequently does not dissolve as much carbonate as it would if it moved more slowly. In the words of Shelford (1925), "The salt content of a water is determined by its age, i.e., the time since it melted from snow or ice or fell as rain, and by the kind of materials over which it flows." So far as the present writer is aware, however, there is little specific data in the literature bearing on this matter. Observations on Boulder Creek showed that although there was a definite relationship between stream flow and bound carbon dioxide, this relation was true only in a general way and could by no means be interpreted as a linear relationship. As indicated in Fig. 3, all bound carbon dioxide determinations of more than 26.0 p.p.m. were associated with low stream flow, usually less than 20 cubic feet per second. Smaller quantities of bound carbon dioxide, however, were associated with a relatively wide range of stream flow, and the smaller the amount of bound carbon dioxide, the greater the range of flow. Between 20 and 25 p.p.m. of bound carbon dioxide, for example, the stream flow ranged from 10.6 to 89.7 cubic feet per second, while between 10 and 15 p.p.m. it ranged from 21.0 to 143.0 cubic feet per second. There are several factors which may be of some importance in producing these wide variations.

First, the precise geographical location of a heavy rain may be significant since the nature of the local surface soil and rocks may determine the amount of carbonate dissolved by the drainage water. Second, the time of the year may be significant; early melting snows and rains may pass over much ice and frozen ground where the solutes are less available than at other times of the year. Third, it is possible that during prolonged rains or thaws the amount of carbonate picked up by the surface drainage in a given area may vary somewhat. Also, it is possible that the occasional diversion of some of the water through the two irrigation ditches may explain instances when a low stream flow was associated with an unusually small amount of bound carbon dioxide.

In any small, unpolluted stream such as Boulder Creek where the water is being continuously aerated, the dissolved oxygen concentration is essentially 100 per cent. Seldom, however, is a determination exactly 100 per cent; usually there is some chance variation on each side of this value. In a series of 30 determinations made on Boulder Creek, oxygen ranged from 91 to 107 per cent saturation, but the average was 100.6 per cent.

One of the outstanding characteristics of mountain streams is the fact that there is considerable variation in the amounts of total dissolved and suspended materials in their waters. Contrary to expectations, the amount of suspended silt in Boulder Creek was rather low, even during periods of high water; the greatest quantity found was only 8.5 mg. per liter. In seven series of determinations the total residue ranged from 44.4 to 120.3 mg. per liter; the ash fraction ranged from 32.8 to 98.8; the loss on ignition had the least variation, the range being only 10.1 to 24.4 mg. per liter. As indicated in Table 1, there

TABLE 1.—Boulder Creek Residues. (mg. per liter)

Date	Total residue	Loss on ignition	Ash	Stream flow c. f. s.
Nov. 11, 1939	82.3	16.6	65.7	81.0
Feb. 10, 1940	87.9	20.3	67.6	
June 11, 1940	80.2	24.4	55.8	115.0
August 14, 1940	44.4 *	10.1	34.3	29.5
Nov. 3, 1940	120.3	21.5	98.8	1.8
Nov. 3, 1940	114.0 *	20.6	93.4	1.8
Dec. 7, 1940	51.7 *	13.5	38.2	16.4
Dec. 23, 1940	46.0 *	13.2	32.8	64.1

(*—water sample filtered)

is no apparent correlation between the stream flow and dissolved and suspended materials. However, definite relationships probably do exist between water chemistry on the one hand, and stream flow, time of year, melting snows, and the intensity and distribution of rainfall on the other hand. Unquestionably these relationships are exceedingly complex, and only a continuous, careful, and extensive investigation would serve to establish their relative importance.

Zooplankton

Although the zooplankton of large, slow-flowing rivers has been studied by many investigators, the zooplankton of mountain streams has been almost entirely neglected, and while it is well-known that the former environment may support enormous zooplankton populations, the latter is frequently said to support either an insignificant population, or none at all. In general, Boulder Creek contained very few zooplankton organisms; compared with larger, slow streams, it had an almost negligible plankton. Those species which were found, however, are the ones which characterize larger rivers and bodies of standing water everywhere.

A significant feature of the Boulder Creek zooplankton was its great variability in both numbers and composition. As shown in the curve for Rotatoria in Fig. 4, for example, ten out of thirty samples contained no

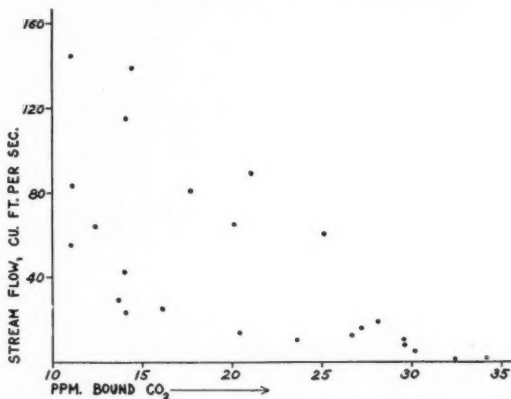


Fig. 3. Relation between stream flow and bound carbon dioxide in Boulder Creek at Boulder, Colorado.

rotifers, and in only five samples were they present in appreciable numbers. *Keratella quadrata* was the most common species, being relatively abundant on November 18, 1939, and September 11, 1940, when there were 240 and 18 specimens per ten-liter sample, respectively. *Brachionus calyciflorus* accounted for the peaks in the curve on June 11 and July 14, 1940, while *Polyarthra trigla* was relatively abundant on December 7, 1940. A few scattered specimens of *Keratella cochlearis* occurred in some samples, and *Synchaeta* sp. and *Monostyla lunaris* were rare.

The irregular curve for the Copepoda (Fig. 4) includes all mature and juvenile specimens of *Cyclops bicuspidatus* except the nauplii stages. This species was most abundant during November, December, and January of 1939-

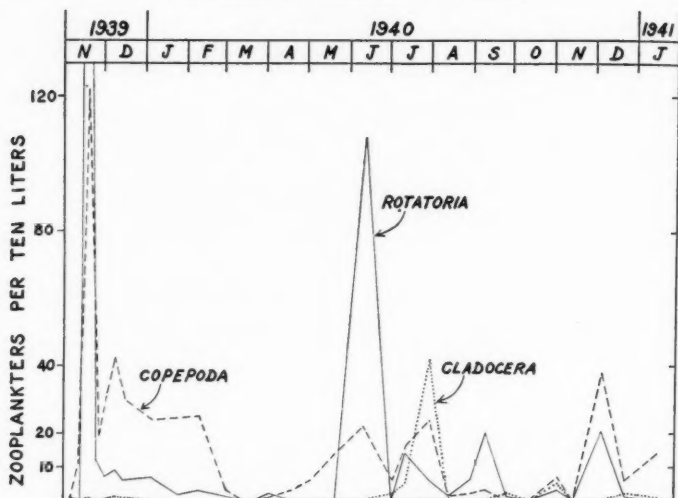


Fig. 4. Zooplankton distribution in Boulder Creek at Boulder, Colorado.

1940. The maximum population found was 122 specimens per sample on November 18, 1939. The largest population found during the summer months was only 24 individuals per sample on July 31, 1940. Six of the 30 samples contained no copepods.

Nauplii ranged from 0 to 100 per ten-liter sample and were most abundant during December, January, February, April, May, and June.

The occurrence of Cladocera was extremely sporadic. On July 31, 1940, 42 specimens per sample were found; 36 of these were *Bosmina* and 6 were *Daphnia*. The next highest population was only 5 *Daphnia* per sample on November 3, 1940. Twenty of the 30 samples contained no Cladocera.

The few *Centropyxis* spp. and small *Diptera* larvae which were found in the plankton had of course been dislodged from the stream bed by the current.

Although the curves in Fig. 4 show poorly-defined zooplankton maxima during the winter of 1939-1940 and the summer of 1940, it should be borne in mind that these do not necessarily represent typical annual population trends. The curves have been drawn in merely to indicate the variability of zooplankton populations as shown by random and infrequent sampling. The demonstration of definite population cycles or trends would require very frequent sampling, since it is likely that the quality and quantity of the zooplankton may vary considerably from day to day. The "average" populations of zooplankters given above, therefore, are of no statistical significance, but are presented simply to indicate roughly the numbers of organisms which may be present in such a stream as Boulder Creek.

Reinhard (1931) and Galtsoff (1924), as well as many previous workers, maintained that there is a more abundant development of plankton organisms during periods of low water, and that the addition of barren storm waters and the consequent increase in the velocity of the current are accompanied by a pronounced decrease in the plankton. While these generalizations may be applicable to larger streams and rivers, there is no evidence from the standpoint of the present brief investigation that they are true of Boulder Creek where the zooplankton population is almost always negligible, regardless of the current. Indeed, there do not appear to be any significant, obvious correlations between zooplankton and stream flow, temperature, or any other ecological factor. Similarly, there seems to be no adequate explanation of the sporadic variability of the zooplankton, and it is especially difficult to attempt to account for the complete absence of copepods, Cladocera, and rotifers in so many of the samples.

In contrast to the older supposition that the *potamoplankton* consists of a group of plankton organisms found only in running waters, most hydrobiologists are now agreed that the river plankton contains few or no species peculiar to it, and that it is not a particularly characteristic assemblage of limnetic organisms. Rather it is composed of forms which are usually more or less common in lentic environments plus quantities of littoral or benthic forms swept along by the current.

The phenomena associated with the origin of the zooplankton population of a stream have not yet been conclusively established. While it is well-known that swift-flowing headwaters of streams and rivers have no measurable plankton, it is rather difficult to account for the gradual increase in the plankton farther downstream. Krieger (1927) maintained that the organisms constituting a river plankton are derived from (1) the areas surrounding the headwaters of the river; (2) from pools along the river where there is only a slight current; (3) plankton derived from lakes along the course of the river; and (4) tributary streams and drainage. More recently Butcher (1932) has shown that the river bed itself is a very important source of the plankton, particularly the algae (see below). As emphasized by the latter author, however, Krieger's sources (1) and (4) are of doubtful significance; in fact, Krieger himself stated that the ultimate headwaters of a river are without plankton, and that the algae of source bogs and marshes are soon destroyed upon entering the stream. With reference to (4), tributaries and drainage must have a source just as well as the main stream; consequently such considerations only extend the matter farther up the water course. While there is a chain of small lakes on North Boulder Creek near the Continental Divide, they are certainly of no importance so far as the zooplankton organisms collected at the sampling station are concerned. The zooplankters of these lakes are mostly *Diaptomus*, *Holopedium*, and *Notholca*, none of which were found in the stream samples. About two kilometers above the hydroelectric station, however, the water by-passed from Barker Reservoir goes through a retaining pond having an area of 4.9 hectares, where large populations of *Polyarthra*

trigla, *Bosmina longirostris*, and *Cyclops bicuspidatus* were common. Although it is possible that this pond may be a source for these three forms, there must be still another source for *Daphnia longispina*, *Keratella cochlearis*, *Brachionus calyciflorus*, and *Keratella quadrata*, all of which were relatively common in the stream but absent from the pond. Obviously these four species, as well as others, must have originated in the stream itself, and in spite of the fact that the greater portion of the stream consists of rapidly flowing water, there are many small pools in which the water is relatively quiet and where a small but changing population of zooplankters could reproduce sufficiently to contribute a significant population to the main stream. Indeed, with respect to this postulate, the fact that the great majority of the Cladocera and Copepoda collected were immature forms may indicate that the sampling station was situated near the upper geographic limit of these transient pool populations. On the other hand, the turbulence of the stream and the consequent friction of the organisms upon the stream bed and upon suspended particles probably were responsible for the destruction of large numbers of both mature and immature zooplankters, the remains of which were sometimes abundant in the trap samples. In this connection, Galtsoff (1924) found that the Rock Island Rapids of the Mississippi, which are about eight miles in length, destroyed sixty per cent of the plankton.

Although no measurements were made, it is estimated that water leaving the lowest lake along North Boulder Creek drainage high in the montane zone would take less than fifteen hours to reach the sampling station at the base of the foothills. In view of the extreme "youth" of this water, therefore, it is surprising that the stream contained as many zooplankters as it did. Eddy (1932) found no plankton in the uppermost 50 miles of the Sangamon River, Illinois, where the water is much older and where the turbulence is much less pronounced than it is in mountain streams.

Phytoplankton

The characteristics of the phytoplankton of Boulder Creek corresponded closely with the generalizations of des Cilleuls (1928) concerning rapid streams: (1) at all times diatoms were the dominant phytoplankters, quantitatively and qualitatively; (2) the phytoplankters comprised only a few species; and (3) the phytoplankters greatly dominated the zooplankters.

The most abundant diatoms were *Melosira*, *Asterionella*, *Synedra*, *Navicula*, *Stauroneis*, *Diatoma*, and *Gomphonema*. While the first three of these are true phytoplankton genera found in many types of aquatic environments, there were species of other genera which are normally found growing on the rocks and pebbles of the stream bed. In some of the phytoplankton samples sessile diatoms were more abundant than the true phytoplankton forms. Aside from the diatoms the only other phytoplankter was *Ulothrix* spp. Like many diatoms, this filamentous alga normally is attached to the stream bed. As emphasized by Butcher (1932), however, quantities of sessile forms are continuously being torn loose from the substrate to become a large portion of

the plankton. Since many of these algal cells were dead, great care was taken in counting the samples to include only apparently healthy cells.

Like the zooplankton organisms, the diatoms and *Ulothrix* varied greatly in their abundance. The former ranged from 9,000 cells per liter on November 16, 1940, to 2,574,600 cells per liter on May 3, 1940. The latter was absent in the samples taken on October 13 and November 16, 1940, but reached a maximum of 16,630 cells per liter on January 18, 1941. Although the irregular logarithmic curves in Fig. 5 are derived from a relatively small amount of data, there is a rather definite phytoplankton maximum between April and

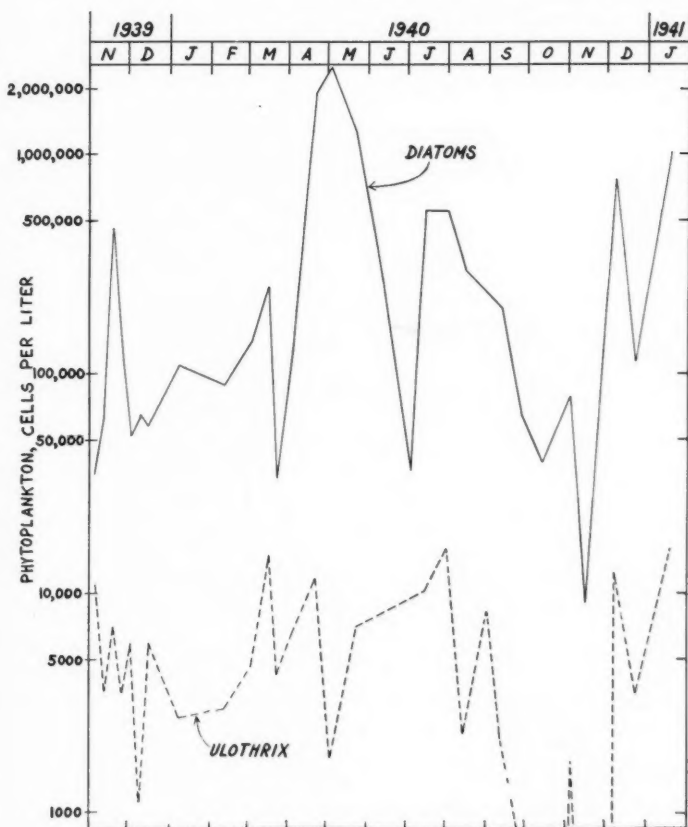


Fig. 5. Phytoplankton distribution in Boulder Creek at Boulder, Colorado.

August. This maximum is probably due to two factors: (1) greater growth and abundance during the warmer months coupled with (2) the fact that the spring and early summer freshets serve to tear more sessile forms loose from the substrate than is the case during the rest of the year. The "average" numbers of phytoplankton organisms throughout this investigation were 443,930 diatom cells per liter and 4630 *Ulothrix* cells per liter.

An analysis of the available data shows that there is no apparent correlation between stream flow and the amount of phytoplankton in suspension. If, however, a definite relationship exists, and it is very likely that it does, particularly in the case of *Ulothrix*, only continuous measurements of stream flow and frequent samples (every hour, for example) would probably serve to demonstrate this relationship.

Summary

Boulder Creek, Colorado, is a typical, small, cascading mountain stream arising from numerous tributaries near the Continental Divide and flowing eastward to the plains. Thirty series of determinations made at the base of the foothills over a period of 15 months demonstrated that several limnological characteristics of this stream varied greatly. Stream flow ranged from 0.9 to 333.0 cubic feet per second; the pH varied from 7.0 to 7.9; bound carbon dioxide from 11.0 to 34.2 p.p.m.; total solids from 44.4 to 120.3 mg. per l.; and temperature from 0.4° to 20.6° C.

The scanty zooplankton consisted of Copepoda (one sp.), Cladocera (three spp.), and Rotatoria (six spp.). Total numbers varied from 0 to 362 per ten liters of water; the average was 57 zooplankters per sample. It is suggested that the zooplankton originates mainly from small populations inhabiting the deeper quiet pools of the stream.

The phytoplankton consisted entirely of diatoms and *Ulothrix* spp. The former ranged from 9,000 to 2,574,600 cells per liter; the latter ranged from 0 to 16,630 cells per liter. Much of the diatom population and all of the *Ulothrix* were derived from the surface of rocks and pebbles of the stream bed.

Evidence is presented which suggests that the distribution and intensity of rains and melting snows at higher altitudes are associated in an exceedingly complicated manner with the limnological variables measured at lower altitudes.

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A Quantitative Faunal Investigation of a Cold Spring Community

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Introduction

The site of Tyee Springs on the Wind River in southwestern Washington was selected by the Fish and Wildlife Service in 1937 as a suitable location for the establishment of a fish-cultural station for salmon and trout. The proposed program of station operation called for the utilization of water from both the springs and the Wind River in the artificial hatching and rearing of the fish. It was also proposed to develop the upper part of the stream, formed by the springs, as a natural rearing area for the fish. This proposed program necessitated a quantitative investigation of the springs and river water and the fauna of the springs-stream community. Samples of the water and fauna were taken in the summers of 1937 and 1941 and the spring of 1938.

Although originating in a practical motive this investigation yielded scientific data on the fauna of a cold spring community and made possible the development of a new and efficient apparatus for the volumetric sampling of aquatic habitats. The scientific results from the investigation form the basis of this paper.

Description of Springs and Stream

Tyee Springs bubble up through the floor of the coniferous forest near the banks of the Wind River about 16 miles above its mouth. A graphic description of the springs and the stream formed by them is given in Figure 1.

The springs stream is approximately 1200 yards in length, 50 feet in width and from 6 inches to 3 feet in depth. It may be divided into two parts with reference to gradient and type of bottom.

The gradient in the first 850 yards of the stream, from the springs to the highway, is low and the original gravel bottom is covered for the most part with a layer of mud and wood refuse over which has grown a dense mat of vegetation. Below the highway the gradient is rather steep and the water flows swiftly over a rocky bottom. There is very little vegetation in this part of the stream.

The vegetation in the vicinity of the springs above station 4, see figure 1, was removed by the Civilian Conservation Corps. The character of the denuded bottom in this area and the regrowth of the vegetation over it gave an insight into the probable origin of the peculiar physical conditions in the upper part of the stream.

The original bottom in the first 850 yards of the stream apparently consisted of coarse to fine gravel and sand composed mostly of the volcanic rock which forms the immediate subsurface layer in the region. Silt, washed into the stream from the clay banks, settled out in the slow current and together with the fibrous roots of the vegetation formed a soft flocculent layer of mud over the gravel bottom. This layer at present varies from a few inches to two feet in thickness and with the exception of the areas just below the springs

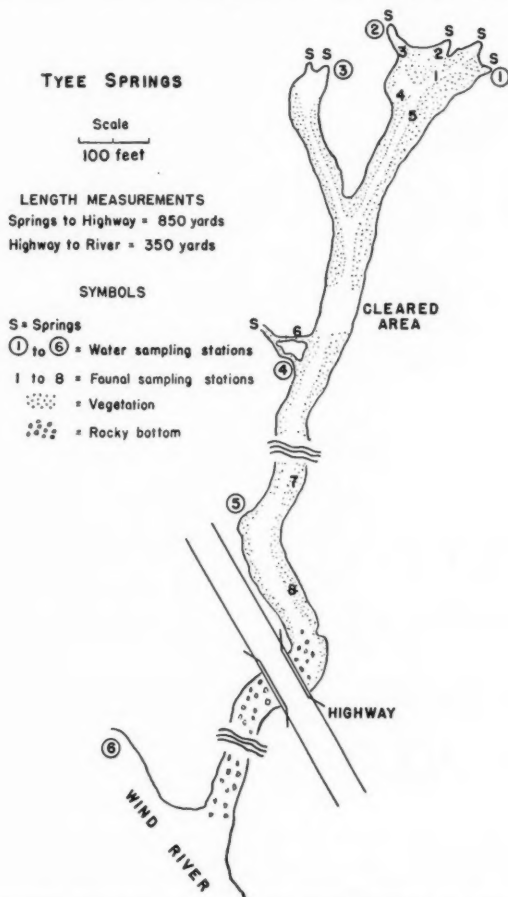


Fig. 1. Graphic description of Tyee Springs showing location of springs, water and faunal sampling stations, and vegetation present in August 1941.

and in the midstream channel, it practically covers the entire bottom. A considerable quantity of decaying wood refuse (chunks, chips and bark) occurs in this layer of mud and also over the gravel bottom. This material was deposited in the stream during the early logging operations in the region.

According to the classification of springs by Bornhauser (1913) there are torrent springs and pool springs. The torrent springs emerge in a rushing stream and the water flows quickly away over a steep rocky bed. The pool springs emerge in a perpendicular rising stream and the water fills a basin before flowing away. Tyee Springs fall in the second classification for, although the upper part of the springs stream is not a true basin, the current is slow and similar environmental conditions prevail.

Ecologically, the community in the upper part of the springs stream would be classified, according to Shelford and Eddy (1929), as a sluggish water stream community on account of the slow current and soft bottom. However, as will be shown later, many of the animals present are characteristic of swift water habitats. The aquatic plants in the community form a water-celery (*Oenanthe sarmentosa*) and monkey-flower (*Mimulus guttatus*) associates, with the willow-herb (*Epilobium adenocaulon*) a subdominant and the grass (*Glyceria pauciflora*) and cress (*Nasturtium officinale forma sisifolium*, Stend) minor influents. The bryophyte *Drepanocladus*, the green algae *Oedogonium*, *Mougeotia*, *Rhizoclonium*, *Vaucheria*, *Spirogyra*, *Ulothrix*, *Uronema*, *Chlorococcum* and *Schizogonium* and a number of the blue green algae including the colonial *Nostoc* occurred in abundance throughout the stream. The dense growth of vegetation in this part of the stream, see Figure 2, is rather remarkable in view of an average water temperature of 45° F. the year-round.

Sampling Stations

The locations in the springs stream and Wind River at which the water samples were taken are indicated in Figure 1 and numbered from 1 to 6. The locations at which the faunal samples were taken are also indicated in Figure 1 and numbered from 1 to 8. The character of the stream bottom and the vegetative covering at these stations were as follows: *Stations 1, 2 and 3.* The stream bottom at these stations was composed of coarse gravel covered with a layer of decaying wood fragments and bark. In 1937 there was very little vegetation in the vicinity of these stations due to the previous clearing operations by the Civilian Conservation Corps. In 1938 about half of the vegetative covering had returned to the area and in 1941 it was almost completely overgrown. In 1937 and 1938 the samples collected at these stations were taken in open water. In 1941 they were taken in the narrow channels. *Station 4.* The stream bottom at this station was composed of fine sand with a small amount of silt. The vegetation consisted of the grass (*Glyceria pauciflora*) in which the sample was taken each year. *Station 5.* The stream bottom consisted of coarse gravel covered with a 2 to 4 inch layer of decaying wood refuse in which some sand and silt had settled. A thick mat of water-celery (*Oenanthe sarmentosa*) covered the area in which the samples were taken each year. *Stations 6, 7 and 8.* The stream bottom at these stations was composed of a



Fig. 2. Tyee Springs and steps in operation of volumetric aquatic sampler. No. 1.—Springs stream in vicinity of stations 1 to 5 in August 1941. No. 2.—Sampling cylinder set in vegetation. No. 3.—Sieve cylinder showing leaf valve in open position. No. 4.—Washing silt from sample by rotating sieve cylinder in clear water of springs stream.

soft, flocculent layer of silt and root fibers varying from 8 to 16 inches in depth. A considerable quantity of wood refuse and chunks of logs was distributed in this layer of mud. The vegetative covering consisted of a mixture of water-celery (*Oenanthe sarmentosa*) and the monkey-flower (*Mimulus guttatus*) with a sprinkling of willow-herb (*Epilobium adenocaulon*). The samples were taken in the vegetation each year.

Methods

Physico-chemical analyses.—The water was analyzed quantitatively for carbon dioxide, dissolved oxygen, soluble phosphorus (P_2O_5) silica (SiO_2) and alkalinity as $CaCO_3$ (methyl orange and methyl red indicators). Temperature readings were taken and the hydrogen-ion concentration was determined by the Beckman potentiometer.

Faunal sampling.—In order to secure an accurate sample of the animal life in the stream and on the vegetative covering it was necessary to devise a method that would make possible the collection of all the animals distributed vertically over a given area of bottom, on the bottom and within it to a depth of approximately 4 inches. In 1937 the samples were taken with the following apparatus: a sheet metal cylinder 13.5 inches in diameter and 30 inches long, a 2 inch suction pump and a 10 inch fine mesh pan screen. The cylinder was dropped over the vegetation and forced from 6 to 8 inches into the stream bed. This operation corralled all of the animals in the water and on the vegetation over a square foot of bottom and also within the bottom to a depth of 4 inches. After fixing the cylinder in place, the vegetation was removed and washed free of macroscopic animal life. Following this operation, 4 inches of bottom material were removed and placed in a separate container. During these two operations many animals were sloughed off into the water as the materials were removed. These animals were not lost but remained corralled within the cylinder. The next operation consisted of removing them from the cylinder by means of the 2 inch suction pump. Owing to the seating of the cylinder 6 to 8 inches in the bottom a fairly good water seal was formed and the cylinder could be quickly pumped dry thus removing all of the animals sloughed off in the first two operations.

The time required for the removal of the sample from the water by this method was relatively brief but the time required for freeing it of excess silt and water and preparing it for preservation was entirely too long. Therefore, a new sampling apparatus was designed for the purpose of speeding up these secondary operations. A new cylinder of the same size as the original sheet metal cylinder was constructed of brass, accurately rolled and fitted with teeth on the lower edge so as to facilitate its seating in the stream bed. Another cylinder of the same length as the first cylinder but slightly smaller in diameter, so that it made a close sliding fit into it, was constructed of perforated brass, 529 holes per square inch, and equipped with a rotary leaf valve at one end. This cylinder functioned as a large strainer or sieve and was used to remove the animals remaining in the water within the sampling cylinder after the vegetation and 4 inches of bottom had been removed. The operation con-

sisted of dropping the perforated or sieve cylinder, valve open, into the sampling cylinder and closing the valve when it hit the bottom. Owing to the close fit of the sieve cylinder into the sampling cylinder practically all of the water in the latter was forced through the valve in the former and completely enclosed within it when the valve was shut. In lifting the sieve cylinder, valve closed, out of the sampling cylinder all of the water quickly drained off. The sieve cylinder functioned with an efficiency of 90 per cent in removing the animals within the sampling cylinder.

If the sample material contained a large amount of silt, it was removed readily by placing all of the material in the sieve cylinder, valve closed, and rotating it in the clear water of the stream. Samples that required from 40 to 60 minutes to collect, clear and concentrate with the first apparatus used, were obtained and prepared in 20 to 30 minutes with the two cylinder apparatus. The operation of these cylinders in the taking and clearing of a sample is illustrated in Figure 2. Wilding (1940) previously described the details of their construction.

The number of samples collected at each of the stations, see Figure 1, in the three years of sampling is given in Table 2. One sample was taken each year at stations 1, 2, 3, 4 and 6, making a total of 3 each for these stations. The sampling at station 5 was omitted in 1938 thus making a total of 2 samples for this station. The sampling at station 7 was omitted in 1941 but three were taken in 1937 and one in 1938 thus making a total of 4. Three samples were taken at station 8 in 1937, two in 1938 and one in 1941, there being six samples in all.

Results and Discussion

Physico-chemical components of waters. — The chemical analysis of the spring water given in Table 1 shows that it contains an abundance of the important constituents necessary for the production of animal and plant life. The phosphorus (soluble) and silica contents are comparable to the maximum quantities of these constituents reported by Juday, *et al.* (1931 and 1938) for the productive lakes in Wisconsin. The dissolved oxygen content is relatively high and the free carbon dioxide content relatively low for most spring waters. Juday, *et al.* (1935) reported the free carbon dioxide content of Wisconsin spring water with a pH of 6.2 as 13.0 mg/l and the average free carbon dioxide content of Wisconsin well waters within a range of pH 6.5-6.9 as 15.7 mg/l. There is some indication of the utilization of the free carbon dioxide and phosphorus in the springs stream for at the lower end of the aquatic plant area, station 5, the amount of these constituents in the water was less than at the springs source. The Wind River water had a higher temperature than the springs water but a lower free carbon dioxide, phosphorus (soluble), and silica content.

Animal community classification. — The different animals and their quantitative occurrence at various locations in the upper or low gradient part of the springs stream are given in Table 2, together with the type of waters found in their normal habitats. From an inspection of this table it will be seen that the

TABLE 1.—Physical and chemical components of the waters of Tye Springs and the Wind River at the Springs site. August 1937 and 1941.

Analysis	Sampling Stations*					
	1	2	3	4	5	6
Temperature in ° F.	44.7	44.8	45.1	46.1	45.9	55.8
Free carbon dioxide in mg/l	7.4	7.7	7.7	7.7	5.5	3.1
Dissolved oxygen in mg/l	10.3	10.0	9.5	9.9	10.4	9.9
Soluble phosphorus (P_2O_5) in mg/l	0.032	0.024	0.016	0.016
Silica (SiO_2) in mg/l	16.0	16.0	11.0
Alkalinity as $CaCO_3$ in mg/l						
Methyl orange	24.1	23.6	23.6	23.0	23.3	26.5
Methyl red	15.5	15.0	14.5	15.0	16.5	20.0
Hydrogen-ion concentration (Beckman potentiometer)	6.95	6.90	6.90	6.90	7.15	7.45

* Stations 1 to 5 were located in the upper part of the springs stream. Station 6 was located in the Wind River just above the mouth of the springs stream.

animal community in this part of the stream is composed of a varied population of typical lotic and static water forms together with those normally occurring in both types of environment. For example, the Plecoptera and Ephemeroidea are characteristic of running waters, whereas the Crustacea and Oligochaeta are typical pond forms. Some of the genera listed under the Trichoptera and Diptera are still water residents while others are found only in running water. Therefore, from the strictly animal standpoint, this community cannot be classified as either a sluggish water or swift water stream community.

The sluggish current, soft bottom and dense vegetation no doubt account for the presence of representatives from the animal groups which are normally found in slow moving or still waters. However, the presence of typical swift water insects such as the Plecoptera and Simuliidae cannot be accounted for except on the basis of the low stream temperature. In fact the low water temperature may also be responsible for the absence of the dragon and damselflies, backswimmers and water boatmen which are so common in slow and still waters.

Owing to the rather definite stratification of the animals in the stream, no single form or group of forms could be designated as the dominants in the community. For example the vegetation above the water was dominated by the pulmonate snails whereas the gill breathing snails, the finger-nail clams, midge larvae and scuds dominated the vegetation in the water. Most of the larvae and nymphs of the insects were found on the bottom; of these the stone fly nymphs were probably the most influential in this stratum both on account of their abundance and predacious habits. Within the bottom strata the aquatic earthworms were the dominant animals. The forms that were active both on the bottom and in the water among the plants were the scuds, water mites and adult beetles.

TABLE 2.—The fauna of Tyee Springs as determined from quantitative samples taken in 1937, 1938 and 1941.

Animals	Average No. of animals in volumetric sample*								Waters in Normal Habitat**
	1	2	3	4	5	6	7	8	
Turbellaria Planariidae	...	9	11	6	Both
Oligochaeta Tubificidae	92	65	9	81	29	33	161	241	Both
Lumbriculidae	7	12	...	3	17	11	...	1	Static
Hirudinea	1	17	...	Both
Crustacea
Ostracoda Cypris	3	15	Static
Isopoda Asellus	5	5	1	Static
Amphipoda Eucrangonyx	1	...	5	21	24	183	42	46	Static
Arachnida Hydracarina	...	5	2	29	2	2	...	1	Static
Insecta
Plecoptera Nemoura	1	5	4	...	20	5	32	20	Lotic
Alloperla	11	5	10	...	5	...	27	...	Lotic
Isonychia	1	4	5	37	8	...	32	7	Lotic
Ephemeroptera Habrophleboidea	...	3	39	35	2	20	86	31	Both
Ameletus	1	5	...	12	...	14	Both
Stenonema	1	...	3	...	22	Lotic
Baetis	5	13	Lotic
Drunella	1	1	...	1	Both
Ephemerella	1	1	Both
Hemiptera Mesovelina	6	1	Both
Neuroptera Sialis	1	Static
Trichoptera Lymnophilidae	24	4	4	6	...	27	23	14	Static
Sericostomatidae	1	1	1	1	1	Lotic
Setodes	3	7	2	5	6	4	42	40	Static
Psilotreta	11	16	Lotic
Lepidoptera Nymphula	...	1	2	Static
Coleoptera (Larvae & adults)
Dytiscus	2	5	2	11	Static
Laccophilus	1	5	3	5	Static
Haliphus	1	4	1	...	5	1	Both
Diptera (Larvae)
Chironomidae	33	93	103	423	89	372	352	445	Both
Tipulidae	3	2	3	8	...	16	21	7	Both
Simuliidae	17	...	Lotic
Dixidae	6	Static
Tabanidae	...	1	Both
Gastropoda
Pulmonata Planorbis	11	15	32	229	354	202	27	57	Both
Helisoma	6	26	...	104	324	137	90	23	Both
Lymnaea	1	8	3	16	...	3	Both
Pectinibranchiata Paludetrina	8	12	18	11	8	109	...	10	Both
Amnicola	11	21	...	Both
Goniobasis	...	1	Both
Lamellibranchia Sphaerium	27	22	...	48	72	154	165	186	Both
Amphibia Triturus	1	...	1	Both
Pisces Cottus	1	2	2	Both
Total	245	315	250	1101	979	1342	1169	1186	
Number of Samples	3	3	3	3	2	3	4	6	

* The volumetric sample included the animals in the water and on the vegetation over a square foot of bottom and to a depth of approximately 4 inches in the bottom. For apparatus used see Fig. 2.

** Taken mostly from Needham and Needham (1938) and Morgan (1930).

A qualitative microscopic study of the bottom deposits showed the presence of the diatoms *Navicula*, *Fragilaria*, *Tabellaria*, *Meridion* and *Diatoma*, the protozoans *Paramecium* and *Stentor*, the crustacean Cyclops and a number of different rotifers.

Animal abundance.—The difference in the animal occurrence throughout the community was primarily quantitative and not qualitative. For example in Table 2 the total average number of animals collected at each of the first three stations (1 to 3) was considerably lower than the total average number collected at each of the other stations (4 to 8), yet the taxonomic groups represented were practically the same at all of the stations. The smaller number of animals at stations 1 to 3 is believed to have been due to the prior removal of the vegetation in the surrounding area thus reducing it to a younger stage than that existing at the other stations.

The average total number of animals at stations 1 to 3, inclusive, and 4 to 8, inclusive, for 1937, 1938 and 1941 were as follows:

Stations	1937	1938	1941
1 to 3	96	248	463
4 to 8	1100	1138	1271

The abundance of animals at stations 1 to 3 increased with the return of the vegetation to the area from a practically denuded condition in 1937 to an almost completely overgrown condition in 1941. This change in faunal abundance is in marked contrast to the more or less stable abundance at the other stations during the period.

Since the stream in the vicinity of stations 4 to 8 was not disturbed prior to 1937 the biotic conditions at these stations may be assumed to be representative of the more permanent habitat. The abundance of animals at stations 1 to 3 will no doubt increase as the stream bed approaches the permanent stage but owing to the close proximity of the area to the springs the abundance may never attain the level of that at the other stations.

Although the samples in 1938 were taken in May and those in 1937 and 1941 were taken in August there was very little difference in the total abundance or the numbers in the taxonomic groups represented in these two seasons. The scuds and snails were slightly less numerous and the caddis fly and midge larvae somewhat more numerous in the May as compared to the August samples.

The biotic conditions in Tyee Springs are in direct contrast to those in the cold springs of central Europe. Hesse, *et al.* (1937) in describing these springs state that the fauna in them is sparse because of the small amount of available nutritive material. He reported the presence of a comparatively few species in them with *Planaria alpina*, the snails *Bythinella* and *Lymnaea*, *Gammarus pulex* and a number of mites as the characteristic forms.

Summary

Tyee Springs bubble up through the floor of the coniferous forest near the banks of the Wind River in southwestern Washington. Their flow is fairly constant and the water temperature fluctuates only slightly around 45° Fahr. The oxygen, soluble phosphorus and silica contents are exceptionally high and the free carbon dioxide content equally low for most spring waters.

The springs form a small stream that empties into the Wind River. The gradient in the first 850 yards of the stream is very low and the bottom is covered with a soft mud over which has grown a dense mat of vegetation. The fauna in this part of the stream consists of a varied population of animal forms some of which are normally found only in lotic and others only in static waters. It is believed that the physical conditions in the stream are responsible for the presence of the static water forms and the low stream temperature for the presence of the lotic water forms.

The number of animals over a square foot of bottom area and within it to a depth of 4 inches was determined at various locations throughout the low gradient part of the stream during the summers of 1937 and 1941 and the spring of 1938. A new and efficient apparatus was developed for the volumetric collection of the animals in this unit of the stream.

The fauna in the older and more stable parts of the community was very abundant, averaging 1170 animals per volumetric unit for the three years of collections. The biotic conditions in Tyee Springs are in marked contrast to those in the cold water springs of central Europe.

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Life History and Distributional Studies on *Eubbranchipus serratus* Forbes (1876)¹

Ralph W. Dexter and M. S. Ferguson

Introduction

During the late winter and spring of 1936 and 1937 the writers made a field study of the anostracan phyllopods occurring in the vicinity of Urbana, Illinois. Extensive field surveys were conducted and intensive collections made from one pond for experimental purposes. Special attention was directed toward the distribution, life history, and rate of growth in the ponds from the hatching of the eggs into metanauplii until the attainment of sexual maturity of the anostracan fairy shrimp *Eubbranchipus serratus* Forbes (1876), a form commonly found in Illinois and also reported from Missouri and Nebraska. Additional observations on the survival and growth of this form were made on individuals taken into the laboratory and maintained there at controlled temperatures. Collections other than near Urbana were made north to Rantoul, west to Monticello, east to Gray's Siding, and south to Savoy and Homer Park.

Recent records of anostracan phyllopods have been reported for eastern North America by Johansen (1921, 1922, 1923, 1926), Garman (1924), Van Cleave (1928), Creaser (1929, 1930, 1931), Geiser (1933), Ferguson (1935, 1939) Mattox (1936), Ferguson and Mattox (1939), and Ward (1940).

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Field and Laboratory Methods

Specimens of *E. serratus* were collected in the field with a fine mesh plankton tow net, small hand net, and dip net. A sample of each collection was preserved in 70° alcohol for later identification and measurement to determine the size and rate of growth in the ponds. Over thirty temporary pools, ponds, and ditches, and five permanent ponds within a twenty mile radius of Urbana were investigated. Collections were made over a period of nine weeks, and from one particular pond (Pond A near Brownfield Woods) thirteen separate lots of fairy shrimps were taken with at least one collection being made each

¹ A contribution from the Zoological Laboratory of the University of Illinois.

week during the spring of 1936. Individuals from the latter pond were studied intensively as to abundance, rate of growth, and seasonal distribution, and some were preserved immediately after collection for subsequent measurements under the microscope, using a micrometer ocular. The remainder of the animals, a representative sample of the collection, were placed in large glass culture dishes and kept in temperature chambers (8° , 10° , and 13° C. respectively) for a study of survival and further growth under uniform laboratory conditions of temperature, daylight, and food supply. Whenever a new collection of fairy shrimps was brought into the laboratory, some or all of the individuals from the preceding collection which still remained alive in the temperature chambers were preserved for a study of growth under controlled conditions as compared to that in animals which had been developing in the pond.

At the time collections were taken from a pond, observations were made on certain physical factors of the environment—air and water temperatures, presence or absence of ice, hydrogen ion concentration of the water, size and depth of the ponds, and general weather conditions.

Outline of Life History of *E. serratus*

The eggs of *E. serratus* are dropped in the water by the female or remain in the brood-pouch at death. It is commonly believed that with many anostracan fairy shrimps the eggs seem to require a period of drying during the summer and fall and then freezing in the winter before hatching occurs. Hay and Hay (1889) state that eggs of *Eubbranchipus* must be dried before development will take place. Mathias (1926) working on *Chirocephalus*, a closely related genus, found that drying of the eggs was not necessary. Creaser (1931) suggests that drying might be necessary in some cases but not in all. An interesting report was made by Castle (1938) who observed *E. vernalis* to hatch in an aquarium where drying and freezing of the eggs were not possible. Avery (1939) succeeded in hatching eggs from the same species which had been moist, while eggs which had been dried failed to hatch. The writers also failed to get dried eggs of this species to hatch. In this case they had been kept at room temperature for several months and then placed in pond water. Avery also reports that his stock of this fairy shrimp was collected from two pools which had not been known to be dry in seven years. Mattox (1939), working with a Conchostracan phyllopod (*Cyzicus*), obtained hatching of eggs which had been (1) dried (2) kept moist (3) frozen (4) not frozen. The writers know of experimental work still in progress in which the eggs of *E. vernalis* have hatched in the laboratory after drying without freezing, freezing without drying, as well as after drying and freezing.²

When the ice melts during warm spells in the winter or in the spring, the egg of *E. serratus* hatches into a very small metanauplius with large swimming second antennae. Accompanied by a series of molts the metanauplius grows and develops rapidly into the characteristic elongated fairy shrimp with eleven

² Personal communication of Richard Weaver, Department of Biology, University of Akron.

pairs of foliaceous swimming appendages. It swims about on its back in search of food—consisting largely of organic debris and plankton organisms. The bodies of the metanauplii of *E. serratus* and many other anostracan fairy shrimps are a brilliant salmon color when they hatch from the egg while the antennae and swimming appendages are usually much lighter. As the fairy shrimp grows the color changes, becoming a light gray with slight traces of orange in some forms, while in others the body takes on a brilliant green, brown, or reddish brown color. There appears to be some relation between the color of the fairy shrimps and the characteristics of the pond in which they are found. Creaser (1929) has also reported differences of color in *Eubranchipus* taken from different ponds. Pearse (1913) observed sexual dimorphism in regard to color, the males being nearly colorless and the females resembling the bottom materials in color. He correlated these differences observed in *E. serratus* (published under the synonym, *E. dadayi*) with the tendency of the male to remain swimming in the water and the tendency of the female to rest often on the bottom.

* After several weeks of growth, sexual maturity is attained. The sexes are separate and have distinguishing characteristics. Each normal female produces a few dozen eggs covered with a heavy, rough, brown shell. Mathias (1937) has discovered that two kinds of phyllopod eggs are produced, those which hatch immediately and others which are resistant and can withstand desiccation for a long period of time. By the time maturity is attained and fertilization has taken place, the waters are becoming warmer, and the fairy shrimps disappear from the ponds, often very suddenly and rapidly. Creaser (1931) found that the males die off first. After a careful search one may often find dead specimens on the bottom or edge of the pond. Those few individuals which live on for a time tend to go into deeper water and may sometimes be found under the cover of aquatic vegetation, dead leaves, or debris. *E. serratus* was not found by the writers in water over 23° C.)

General Observation on *E. serratus* and its Geographic Distribution in the Urbana District

The examination of over thirty temporary and five permanent ponds in the Urbana region investigated during late March and April of 1936 revealed only two species, *E. serratus* and *E. vernalis*. The latter is a larger form found in the northern parts of eastern United States and southern Ontario, and probably has its western limits of distribution in Illinois and Wisconsin. *E. vernalis* was collected from only three ponds during 1936, was never very abundant and never occurred in the same pond with *E. serratus*. In 1937 *E. vernalis* was not found in any of the ponds studied including the three at Homer Park containing this species in 1936. Observations made on *E. vernalis* in eastern Illinois have been added to those made by one of the writers on the same form in southern Ontario and have been published elsewhere (Ferguson, 1939). Previously, Van Cleave (1928) had reported both of these species from Illinois.

E. serratus was collected in sixteen temporary ponds distributed generally around the Urbana region. When found they were usually abundant. Ten other bodies of water in this region were found to contain no fairy shrimp during the spring of 1936. Many of these were deep pools or permanent ponds. Some of the ponds were visited several times, some only once, and one was studied twice a week during the early spring and later was visited once each week until the fairy shrimps disappeared. Each pond in which *E. serratus* was collected is considered below in regard to its location, size, physical characteristics at the time of collecting, and general observations on the fairy shrimp. It is to be noted that the specimens collected from each pond or pool were of a characteristic size and color. Colorless, gray, salmon, pink, reddish, light brown, and brown populations were found.

Temporary spring pools in woods, fields, along railroad fills and roadsides are very favorable for the presence of anostracan phyllopods. They would probably live in most such locations, at least during some years, if once introduced and in the absence of any serious predator or limiting physical factor.

Ice apparently does not harm them since on several occasions they were found living beneath a coating of one-half an inch of ice over two of the ponds.

Schools of the fairy shrimp collect in shallow water around the edges of the pools among vegetation. Quantitative samples indicated that the largest numbers are found on the leeward side of ponds.

E. serratus, during the metanauplius and adult stages, lived through a range in water temperature from 0° C. to 23° C. and a range in hydrogen ion concentration from 6.6 to 8.2. Ward (1940) found *E. vernalis* in a range from 5.5 to 6.8. Mathias (1937) found that phyllopods in general prefer alkaline waters.

The metanauplii and immature adults were positively phototropic and congregated on the light side of the culture dish.

Similar behavior by fairy shrimps has been reported by Holmes (1910), McGinnis (1911), Pearse (1913) Mathias (1926) and Hsü (1933). McGinnis (1911) demonstrated experimentally that the ventral surface of *Eubbranchipus serratus* is always held facing the light, hence the usual and characteristic up-side-down orientation of these organisms. The mature adults become somewhat negatively phototropic and positively thigmotropic.

McGinnis also showed that *E. serratus* is positively geotropic in light and negatively geotropic in the dark.

1. BROWNFIELD WOODS.—Fairy shrimps occurred in two adjacent ponds located in a pasture about one-half mile north of Brownfield Woods, a large wood lot three miles northeast of Urbana. These ponds are here designated as Ponds A and B.

Pond A. This pond, situated only a few yards from the roadway, was temporary, about five feet deep in the middle, and had a muddy bottom supporting around the edge a growth of short grasses. Several small trees had the

lower parts of their trunks submerged during periods of greatest precipitation, and provided a cover of dead leaves for the bottom of the pond where it was shallow. This was the pond which was most thoroughly investigated and provided the fairy shrimps for the detailed life history and growth study described in parts V and VI. *E. serratus* in this pond, while very small, were a bright salmon color, but gradually this faded and the larger forms became grayish with only slight traces of the previous coloration.

Pond B. A few rods north of Pond A was located a smaller and more shallow pond. Here there was more vegetation such as small shrubs, short grasses, aquatic plants, and an abundant growth of filamentous algae. There was a better floor of submerged vegetation and less suspended matter in the water.

On February 24, hundreds of metanauplii were actively swimming in this pond. Large numbers of mature male and female fairy shrimps were collected on March 28, while on April 25 only eight specimens were taken. A few individuals still remained on April 29. As was noted for Pond A, the full-grown fairy shrimps in this pond were grayish with only slight traces of the former salmon coloration.

2. RANTOUL PONDS.—These were four shallow temporary rain ponds (A, B, C, D) located in depressions between the highway and Illinois Central Railway tracks about fourteen miles north of Urbana near Rantoul. They were long narrow bodies of clear water with a thick floor of dead grasses and herbs. This type of pond was not peculiar to the Rantoul district, for many were to be observed, especially during the spring, as one rode along the highway which ran parallel to the railroad for several miles.

Developing metanauplii were very numerous in all four ponds on March 9, and by March 28 there were large numbers of adult males and females. At first the young fairy shrimps were salmon in color, but later they assumed a brownish color.

3. SEYMOUR PONDS.—Two shallow temporary ponds (A, B) containing *E. serratus*, one on either side of a railway, were located just outside of Seymour some eleven miles west of Urbana. One pond (A) was between the highway west of Seymour and the railway, had a bottom of thick prairie grasses and shrubs, and contained water which was very clear but of brownish coloration due probably to dissolved organic matter. The second body of water (B), smaller, more shallow, and containing much filamentous alga and bordered on one side by low shrubs, was located at the edge of a pasture field on the other side of the railway at a lower level than the other pond. Both pools were about one foot in maximum depth.

One collection was made from these ponds on March 28, and at that time large numbers of mature *E. serratus* were taken. The general color of these forms was a definite reddish brown.

4. MONTICELLO POND.—This was a long and narrow ditch pond along the

roadside near Monticello, about twenty miles southwest of Urbana. There was a yellowish clay bottom, and the water, which was slightly turbid from suspended matter, was less than one foot deep when examined for fairy shrimps. A few dozen mature individuals, light brown in color, were collected here on March 28.

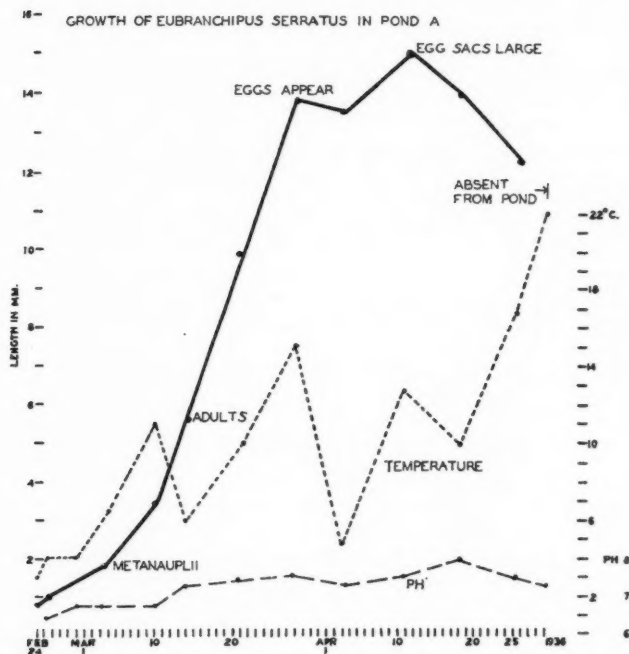
5. TOLONO PONDS.—North of Tolono, about seven miles south of Urbana between the highway and the Illinois Central Railway, fairy shrimps were found in two neighboring, long, shallow, temporary ponds (A, B), similar to those near Rantoul. As was the case with the Rantoul ponds the bottom of each of these ponds was covered with a thick mat of dead grasses. Large numbers of light brown fairy shrimps occurred in these ponds on April 13.

6. SAVOY PONDS.—Just north of Savoy, about four miles southwest of Urbana, was located a series of ponds in a pasture a few yards from the east side of the Illinois Central Railway tracks. The ponds, seven in all, were of varying shapes and depths and all in close proximity to one another. Some of these bodies of water were probably connected at one time and a few of them probably now become continuous at flood times. The largest pond, several yards in diameter, had a muddy bottom but fairly clear water. The smaller ponds, some only three or four yards in diameter, contained clear water and much filamentous algae. Only four of the ponds were found to contain *E. serratus* when visited on April 13. They were light brown in color and showed distinct size variation from pond to pond. None was found on April 29. One fairly large but very shallow body of water appeared to be particularly barren with respect to plankton, and upon investigation it was found that the drain from a nearby stable emptied into it.

7. OAKWOOD POND.—This pond was in a roadside ditch near Muncie, twenty miles east of Urbana. It was "V" shaped and extended around the corner of a field. On April 5 several hundred individuals were taken, all of which were of a general light brown coloration.

Just as the ponds investigated differed as to physical characteristics, variations are also noted with respect to the fairy shrimps inhabiting these ponds. Differences in color and size are noted in individuals from neighboring ponds or those far removed from one another, even when all were collected on the same day, although the specimens from any one pond were generally uniform.

The writers believe that ponds from which their collections of *E. serratus* were made, although they were probably but a fraction of those inhabited by fairy shrimps in the Urbana district, are a representative sample of the various types of temporary bodies of water in which these forms may be found. What the factors are which account for the presence of fairy shrimps in one pond while they are absent in another nearby body this study does not show. Certain physical or chemical disturbances in the pond may cause the complete dying out of a fairy shrimp population and several years to elapse before they become reestablished again. It is reasonable to expect that many of the ponds containing no phyllopods during the season of 1936 would provide suitable environments for fairy shrimps once they were introduced into them.



The rate of growth of the pond specimens gradually accelerated each day until the shrimp became mature. The metanauplii at first grew at a rate of approximately 0.1 mm. per day, then increased to 0.3 mm. per day, and after the tenth of March grew about 0.56 mm. per day. The growth of specimens kept in the temperature chambers was quite uniform, averaging 0.13 mm. per day at 8° C. Mathias (1937) has shown that different parts of the body grow at different rates and that some phyllopods attain sexual maturity before growth is complete. With the rise of temperature in the ponds, the fairy shrimp began to die off rapidly. During this time, however, the laboratory specimens continued to grow and became larger on the average than those found in the ponds at any one time. Here again, we were probably dealing with two different broods.

Packard (1883) recorded the seasonal distribution of a *Eubbranchipus* population over a period of several years. Shelford (1913) described the seasonal life history and succession of *Eubbranchipus* in the Chicago region. Johansen (1923, 1926) described the development and life history of another phyllopod, *Limnetis gouldii* in some Ontario ponds and observed the seasonal

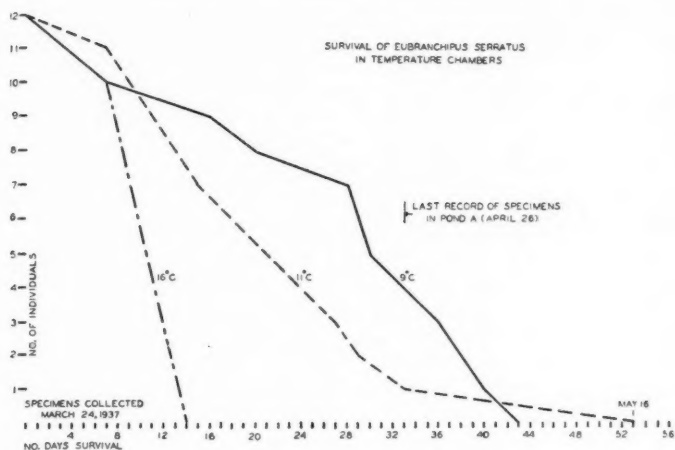
distribution of this species and that of *E. gelidus* (syn. of *Pristicephalus bundyi*) in pools at Ottawa. A morphological study of the development of *Artemia salina* L., and another anostracan, *Branchinecta occidentalis* Dodds, describing the external anatomy and growth of each instar, was published by Heath (1924). Hsü (1933) did the same for *Chirocephalus nankinensis* (Shen). Spandl (1926) published growth curves for a notostracan (*Apus concoloriformis*) and a conchostracan phyllopod (*Leptestheria dehalacensis*). Life history studies of conchostracan phyllopods belonging to the genus *Eulimnadia* have been made by Berry (1926) and Mattox (1937). The latter paper contains a growth curve and data on temperature and pH similar to the one given in this paper.

During the prevernal season, *E. serratus* was the most conspicuous and dominant form of the plankton in Pond A. A single scoop of the dip net would often capture fifty or more specimens. (The physical conditions at the pond during this time are indicated on Figure 1). Later, the copepods *Diaptomus sanguineus* and *Diaptomus* sp. became the most abundant and conspicuous form of the plankton.

Survival of *E. serratus* in Temperature Chambers

During the spring of 1936 specimens of *E. serratus* from Pond A were placed in culture dishes and kept in temperature chambers of 8°, 10° and 13° C. With each collection from the field new cultures were established and a sample of existing cultures was preserved for comparison with the growth and development of the pond specimens. Because of the need for frequent samples for comparative study the cultures were soon exhausted. However, the following observations seemed to be generally true. The individuals kept at 8° C. lived much longer than those at 10° or 13° C. During the first month or so the cultures at 8° C. existed on an average for 8 days, while the later cultures existed longer and in larger numbers. Specimens placed in culture at 8° C. on April 18 lived for 38 days without loss of a single individual, persisting for 29 days after the species could no longer be collected in the pond. The last 3 individuals perished on June 9, 41 days after the last pond collection and after spending 58 days in the chamber.

During the spring of 1937 an experiment was performed to test the survival of *E. serratus* at constant temperature over a longer period of time. Figure 2 presents the results in graphic form. On March 24, 3 cultures (A, B, C) of a dozen individuals were placed in temperature chambers of 9°, 11°, 16° C. Culture C at 16° C. existed for 14 days, with 5 individuals living for 10 days. Culture B at 11° C. was gradually reduced to one survivor in 33 days, at which time specimens in the pond had also succumbed. The surviving individual lived for 20 additional days, until May 16. Culture A at 9° C. persisted with a gradual decline for 43 days, 4 specimens being alive when the final field collection of a few specimens was made on April 26. Three days later no specimens could be found in the pond, but the culture specimens continued for another week, until May 6.



It is interesting to compare the seasonal distribution of *E. serratus* in Pond A for the two successive years. In 1936 adult specimens were first observed on March 14 and were last collected on April 29. In 1937 adult specimens were first collected on March 5 and were present in the pond until April 26.

Because the fairy shrimp developed under a heavy cover of ice during the spring of 1937, the first appearance of the metanauplii could not be determined.

McGinnis (1911) performed temperature gradient experiments with *E. serratus* and found that none of the individuals went above 17° C. When placed at higher temperatures they perished at 28° C. She found the optimum temperature to be between 14°-17° C. Mathias (1937) reported that *Branchinecta paludosa* is not usually found in water over 14° C. On the other hand he discovered that *Artemia salina* could easily tolerate 37° C. and 50% of his experimental animals withstood 39° C. All of them died above 40° C. With *A. salina* 25° C. was found to be most favorable for development. For *Branchipus stagnalis*, 15°-20° C. was most favorable. This species had been kept for several months at temperatures below 20° C. The eggs of phyllopods can withstand extreme high and low temperatures as shown by the experiments of Mathias.

Notes on Annuation

On April 11, 1941, one of the writers (R. W. D.) had the opportunity to revisit many of the collecting stations established for this study in 1936 and 1937. Interesting facts were observed in comparing the fairy shrimp populations and the pools with the situation as reported here for the earlier years.

1. Brownfield Woods, *Pond A*. The pond was half dried up, with a maximum depth of about two and one-half feet. The water line was about two feet below the normal level and the lowest ever seen in the spring by the writer. A small number of *E. serratus* was collected, the smallest sample taken at this station by middle April. *Pond B*. This pond was reduced to a small area of several inches in depth, and the water was very warm. No phyllopods were found although previously they were fairly numerous at this date.

2. Rantoul Ponds. No phyllopods could be found in any of the long chain of pools along the railway tracks. Previously they were common.

3. Savoy Ponds. Three of the four pools from which previous records were made contained an abundance of *E. serratus*, most of which were immature, although a number of mature individuals were collected. The largest pond did not contain any specimens this year, nor did two of the smaller ponds. The polluted pool, as in former years, was void of phyllopods.

4. Oakwood Pond. The "V"-shaped pool in the corner of a corn field near Oakwood had water to a depth of about one foot. Numerous specimens of *E. serratus* were collected under the bottom vegetation and debris. None was observed swimming until disturbed from the bottom. All sizes and life stages were collected.

5. The two ponds at Muncie were visited, but again no fairy shrimps were collected.

6. At Homer Park the pools along the road-fill were completely dried up. The two pools in a pasture woods close to the Salt Fork River contained six to eight inches of water but, as in 1937, no specimens of *E. vernalis* although they were collected in abundance in 1936.

Summary

A field study on the life history and distribution of anostracan phyllopods in the vicinity of Urbana, Illinois, during the late winter and spring of 1936 and 1937, and the spring of 1941 has shown the following:

1. Two species were recorded: (a) *Eubbranchipus serratus* found in great abundance and widely distributed. (b) *E. vernalis* found in three pools at Homer Park during the season of 1936 but not in 1937 or 1941.

2. The color of *E. serratus* was somewhat characteristic of each pool from which it was collected.

3. Curves are presented to show the seasonal life history and growth of *E. serratus* in one pond during the winter and spring of 1936 and survival at constant temperatures in comparison with survival in the pond during the season of 1937.

4. Annual differences in time of appearance and duration, in distribution and abundance are noted between years 1936, 1937 and 1941.

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Food of Some Lake St. Marys' Fish with Comparative Data from Lakes Indian and Loramie

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While seining in Lake St. Marys during the summer of 1940, the writer preserved a large number of specimens, for later study. These specimens were of various species and length groups. Specimens from both Indian and Loramie Lakes were likewise preserved. Acknowledgments are due Dr. M. W. Boesel for his assistance in the preparation of this paper.

With the development of the new science, Fish Management, comes the need of additional information concerning the lives and habits of the fish in our fish populations. Numerous studies have been made on all the species mentioned, but so far as is known to the author, no food studies have been made of the fishes of the lake under consideration. Fish Management principles involve the building up of an increasing food supply to support and mature a greater population of legal-sized fish. With the above thought in mind, the ensuing studies were made.

Methods and Materials

The fish examined were collected near shore in water of about four feet or less in depth. They were taken in both 15 and 50 foot, quarter-inch mesh seines. The specimens were preserved in 5% formalin solutions.

The method of study was a simple one of counting the organisms present in each stomach; or in the case of large numbers being present, the food mass was divided into portions and one portion counted. The total was obtained by multiplying the number present in one portion by the number of portions into which the stomach contents were divided. In such cases, all organisms other than the Entomostraca were counted. The stomach contents were squeezed into a glass dish and examined under a binocular microscope. This gives no quantitative information, only information of a qualitative nature.

Data

LARGEMOUTH BLACK BASS (*Huro salmoides* Lacépède)

A. Lake Loramie—According to the information obtained, over 89% of the food taken was crustaceans, both Copepods and Cladocerans (Table 1). Copepods were more numerous than Cladocerans. Small numbers of midge larvae and other immature insects were taken. Insect food was very consistent in that water boatmen (*Corixa*) comprised the major portion of the immature ones. A very obvious shift from crustaceans to insects, with increase in size of the fish, can be seen.

B. Indian Lake—From Table 1, it can be seen that these fry fed almost wholly (99%) on Entomostraca. In this case the Copepods were in slightly greater numbers than the Cladocerans.

C. Lake St. Marys—Crustaceans comprised 88% of the stomach contents of this series of bass fry. Copepods and Cladocerans were in almost equal abundance. A series of 69 individuals of 3 cm. and less, taken from a single school showed Cladocera and Copepods to be of almost equal importance. Forbes (1903) found 87% of the food of these small bass to be Cladocera. A progressive change in the food, according to the size of the fish, was noted. The early food, Entomostraca, is replaced by insects in the intermediate stage, and later give way to fish and craws in adults. Such a cycle was found by Wickliff and also by Turner and Kraatz (1920). Ewers and Boesel (1935) found a predominance of Entomostracan food with Cladocera more abundant. Ewers (1933) found 87.1% of the food to be Crustacea with Cladocera more abundant.

BLUEGILL (*Lepomis macrochirus macrochirus* Rafinesque)

The bluegills of this series fed chiefly on midge larvae (Chironomidae). Table 1 shows this type of food to represent 59.4% of the total. Copepods also represent an important food item. All bluegills contained midge larvae, with as many as 844 in one stomach. Surprisingly, immature insects constituted only .05% of the total food.

WHITE CRAPPIE (*Poxomis annularis* Rafinesque)

According to the examinations, the white crappies of these length groups, feed almost wholly (97.4%) on Crustacea with Cladocera comprising the major part. In one stomach, Polyphemus reached a peak of 448 individuals. There seems to be little relation between the size and food taken. Ewers (1933) in Lake Erie found Crustacea to make up 96% of the food with Copepods more abundant. Forbes (1903) found over 70% of the food of the individuals examined to be Crustacea but equally divided. Trautman (unpublished work) found 48 stomachs of 52 to contain Entomostraca.

BLACK CRAPPIE (*Poxomis nigro-maculatus* LeSueur)

Table 1 shows that the black crappie fed predominantly on crustacea which made up 98.2% of their food. These were nearly all Cladocerans. Midge larvae were present in many stomachs. Ewers (1903) found the food of this fish to be similar to that of the white crappie and she treated them together. She found over 70% of their food to be Entomostraca.

QUILLBACK (*Carpiodes cyprinus* LeSueur)

Lake St. Marys quillback of this series contained largely Crustacea about equally divided as to numbers between Cladocera and Copepods. Midge larvae

were present in large numbers, almost as numerous as the Copepods or Cladocerans. All stomachs contained large amounts of sand and detritus.

YELLOW PERCH (*Perca flavescens* Mitchell)

Midge larvae and other immature insects formed 86.9% of the fish examined. Peculiar enough is the fact that here, as well as in the other species examined, an overwhelming majority of the immature insects were water boatmen. Only one fish was found that had taken a minnow. Copepods were the only other food organism of importance.

ORANGESPOTTED SUNFISH (*Lepomis humilis* Girard)

Fish of this series were found to feed chiefly on midge larvae and pupae to the extent of 81.1%. Water boatmen were again outstanding in the food mass. Another item of interest is the large number of caddice-fly (Trichoptera) cases of expert masonry found in the stomachs. Only one of the 52 stomachs was empty. Evidences of surface feeding were advanced by the presence of a few winged insects, chiefly ants.

BROWN BULLHEAD (*Ameiurus nebulosus nebulosus* LeSueur)

From the few specimens examined 90% of the food was found to be crustacea and of these Cladocera were most important. Midge larvae and pupae were also found in considerable numbers. Another food item, Ostracods, became somewhat important in this group. Nearly every stomach contained one or more of them. Forbes (1903) found the food of the genus *Ameiurus* to be 74% Chironomous and 18% Entomostraca.

DISCUSSION

In nearly all cases the stomachs contained varying amounts of inorganic materials as well as organic matter in an unidentifiable state. Large amounts of inorganic matter might well be expected in the stomachs of fish feeding to a great extent on midge larvae and pupae. This unidentifiable matter has not been listed due to its lack of bearing on the types of food used by these species of fish.

Only in one or two cases were any filamentous algae found.

Entomostraca formed by far the greatest portion of the food taken by all species of the fish studied. Cladocera and Copepods were found in well over half of the specimens. Most of the Entomostraca were intact, and perfect specimens were found in the feces near the anal opening of many of the fish examined. A great deal of variation in numbers was found. The greatest number in a single stomach was 596 in a 4.7 cm. white crappie. Copepods were found somewhat more abundant than Cladocera, but in general they were present in many stomachs in equal numbers. Large numbers of Cladoceran eggs were present in many of the stomachs.

Quantitatively speaking, midge larvae were without doubt of first importance. They formed an important food item in all species and their greater size would place them above all else in nutritive value. One 14 cm. bluegill's stomach and intestines contained larvae and skulls to the number of 844. The larvae varied greatly in size but only three or four were found that exceeded 7 mm. in length.

As for immature insects other than midge larvae, water boatmen ranked first in importance. As many as 39 nymphs were found in the digestive tract of a largemouth bass 10 cm. long. All species used them in varying numbers.

Some of the rarer and interesting things found in the stomachs of these fish were spring-tails (Collembola) in a brown bullhead, winged ants (Formicidae) in a white crappie, a beetle (Coleoptera) in a bluegill, and a water earthworm (Tubificidae) in another bluegill. Ostracods, Amphipods Plecoptera larvae, Odonata nymphs, Chironomid and Culicid adults. Orthoptera and Plecoptera adults were some of the occasional food items found in these examinations.

The group of 66 individuals taken from one school (Table 1) shows there is little feeding preference in bass fry.

Summary and Conclusions

1. Cladocera were found in the stomachs of all species of fish examined with the exception of the yellow perch.
2. Copepods were found in the stomachs of all species of fish examined with the exception of the orangespotted sunfish.
3. Midge larvae were found in the stomachs of all species.
4. Insect nymphs or adults were found in the stomachs of all species examined.
5. Judging from the 66 bass taken from one school, there seems to be no preference between Copepods and Cladocerans.
6. Bass taken from the three lakes show identical food selection and a close correlation between percentages of food items.
7. All types of fish examined used the same kind of food in their earlier stages.
8. The small number of empty stomachs and intestines seemingly indicate a plentiful food supply.
9. These species are in close competition with each other in their earlier stages of life.
10. Orangespotted sunfish, which are of no value to fishermen, and doubtful value as a forage fish, compete with game fish for food.
11. Competition in their earlier stages show the necessity for controlling the introduction of fish into any lake or pond.

TABLE 1.—Percentage of Food per Species by Count.

Species	No.	Locality	Length	Cladocera	Copepoda	Midge L.	Insect A.	Insect I.	Ostra.	Fish	Amph.	Misc.
L. M. Bass	22	Loramie	1-14 cm.	34.7	55.1	2.2	.07	8.7	.07	.1		
	42	St. Marys	2-15	34.7	46.9	10.	2.9	2.	2.4		.7	Coll. Rotif. .1
	57	Indian L.	1-4	41.2	58.	.04		.01		.1		.4
Bluegill	23	St. Marys	2-15	2.2	36.6	59.4	.06	.5				
Quillback	30	St. Marys	2-10	37.4	36.5	25.6				.07	1.4	Olig. .04
O. S. Sunfish	52	St. Marys	5-10	3.5	81.1	1.8	.2	11.7	1.06	1.7	.2	Olig. .001
W. Crappie	22	St. Marys	1-12	83.	11.7	42.3	.1	44.6	2			Olig. .03
Y. Perch	21	St. Marys	4-11									
B. Crappie	36	St. Marys	1-18	80.9	17.3	1.4		.1	.1	.05		Snail .1
Br. Bull.	15	St. Marys	1-6	70.9	16.1	9.6	.5			.4	.8	
L. M. Bass	66	St. Marys	1-3	51.7	45.4	.4		.07		.6		

Ostra.	Ostracoda	Coll.	Collumbola	Insect A.	Insect Adult
Amph.	Amphipoda	Rotif.	Rotifera	Insect I.	Insect Immature
Olig.	Oligochaeta	Midge L.	Midge Larvae	O. S. Sunfish	Orange-spotted Sunfish

TABLE 2.—Percentage of Stomachs Containing Types of Food.

Species	Locality	Length	Cladocera	Copepoda	Midge L.	Insect A.	Insect I.	Ostra.	Amph.	Fish	Olig.
L. M. Bass	Indian L.	1-4 cm.	96.5	100	17.5		7.		15.8		1.7
	St. Marys	2.5-3.5	100	100							
	Loramie	3.5-14	12.5	9.4	43.7	9.4	25.		9.4	25	3.7
		1-3	100	100	23.5						
		7-14	60	40			80				
B. Crappie	St. Marys	1-18	63.8	58.4	44.4		13.8	5.5		5.5	
Y. Perch	St. Marys	4-11		15.2	33.3		76.2		14		5
W. Crappie	St. Marys	1-15	45.5	31.6	31.6	4.5	18.1			40.9	
Bluegill	St. Marys	2-15	13	30.5	82.2	8.7	37.8	8.7			4.3
Quillback	St. Marys	2-10	13.3	53.3	56.6		3.3	3.3			
O. S. Sunfish	St. Marys	5-10	1.9		69.2	1.9	51.9	1.9		1.9	
Br. Bull.	St. Marys	1-6	66.6	53.3	66.6	13.3	1.9	53.3	1.9		

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Age and Growth of Johnny Darters, *Boleosoma nigrum olmstedii* (Storer) and *Boleosoma longimanum* (Jordan)

Edward C. Raney and Ernest A. Lachner

In this study the scale method was used to elucidate some of the main features of the life histories of two species of small percid fishes. *Boleosoma nigrum olmstedii* and *Boleosoma longimanum*. One of these, the eastern johnny darter, *B. n. olmstedii*, is of considerable importance as food for young yellow pike-perch, *Stizostedion v. vitreum*, in lakes, as was shown in a recent study by Raney and Lachner (1942). We have also observed that it is an important item in the diet of the northern smallmouth bass, *Micropterus d. dolomieu*, in streams of central New York. Some phases of the life history, such as its spawning habits, have been treated by others, and summaries of these studies may be found in papers by Adams and Hankinson (1928) and Atz (1940). As far as we are aware, the scale method has not heretofore been used in the study of any darter. Some generalizations on age of the barred fantail darter, *Catnotus flabellaris flabellaris*, by Lake (1936) and on the spotted darter, *Poeciliichthys maculatus*, by Raney and Lachner (1939) were made by the study of length-frequency curves, based upon large numbers taken at a given locality.

Most of the darters used in this study were collected by the writers during the past five years, although some additional material in the Cornell University Museum collection yielded data on much needed sizes. The specimens were taken in fine mesh seines, preserved in formalin and later stored in alcohol. A total of 845 specimens of *Boleosoma nigrum olmstedii* and 102 specimens of *Boleosoma longimanum* were studied. The *olmstedii* were taken in tributaries of the upper Susquehanna River system near Candor, in Lake Ontario at Fair Haven Bay and in Oneida Lake, New York. Specimens from Massachusetts were made available through the kindness of Dr. Britton C. McCabe. All the specimens of *Boleosoma longimanum* were collected in tributaries of the upper James River system in Virginia.

Determination of Age

Scales taken from the mid-side just above the lateral line were cleaned and mounted in glycerine jelly. After examining many scales under the microscope the practice of mounting scales was discontinued, and they were read while in water in a watchglass.

The scale method has been used in a number of studies of the growth of some of the more important food and game fishes in the family Percidae.

Studies on the pike-perches, *Stizostedion*, have been made by Adamstone (1922), Deason (1933) and Hart (1928), and on the yellow perch, *Perca flavescens*, by Harkness (1922), Hile (1931), Hile and Jobes (1940), Jobes (1933), Schneberger (1935) and Webster (1942). The scales of *Boleosoma* are much like those of *Stizostedion*. The circuli are far apart during summer when growth is more rapid, and, conversely, are closer together in the late fall when little growth takes place. This fact has been established for *Boleosoma nigrum olmstedii* by examining scales taken at one locality at various dates from early spring to late fall. The variation in the distance between the circuli is illustrated (Fig. 1) in the photographs of the scale from a male *olmstedii*. In addition, the growth of the newly hatched young was observed in nature. During the first summer the young showed the type of circulus spacing which may be seen (Figs. 1 and 2) in the part of the scales between the focus and

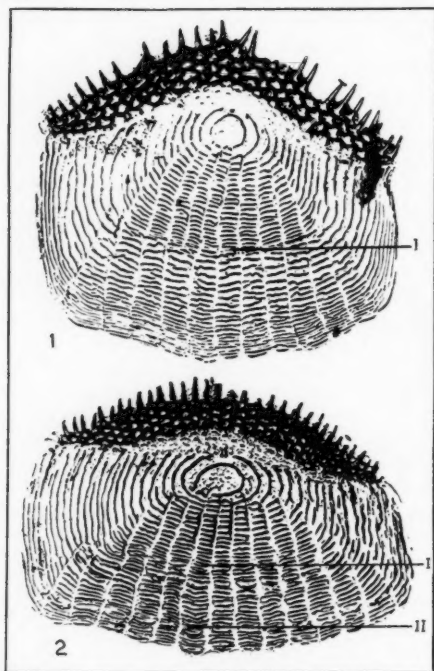


Fig. 1. Scale of an adult male *Boleosoma nigrum olmstedii*, 56 mm. in standard length, collected in Catatunk Creek at Candor, New York, on October 26, 1935. It has just completed its second summer.

Fig. 2. Scale of an adult female *Boleosoma nigrum olmstedii*, 55 mm. in standard length, collected at the same place on October 26, 1935 and which has completed its third summer.

the first year mark. The point on the anterior field of the scale which is laid down between the cessation of growth in the fall and just before the resumption of growth in the spring is interpreted as an annulus, or year mark, and these are designated by Roman numerals in Figs. 1 and 2. There is no evidence of the annulus on the lateral field, such as occurs in yellow perch and centrarchid scales. The second annulus is clear cut and easily recognized on scales of darters which are in their third summer. The scales of a male and a female *olmstedii* of approximately the same length, shown in Figures 1 and 2, are typical of the growth of each sex. The males grow faster, especially during the second summer, so that at the end of the second summer the average length of the male is as great as that of the female at the end of her third summer.

The time in the spring when growth resumes varies somewhat with latitude. The annulus was already formed in all specimens of *Boleosoma longimanum* from the James River system in Virginia during the first week in April. Some growth had taken place, although these specimens had not yet spawned. In *Boleosoma nigrum olmstedii* from tributaries of the upper Susquehanna River system in the vicinity of Candor, New York, growth has usually resumed, and the annulus has formed during the first two weeks in

TABLE 1.—Length frequencies for each age group of 340 specimens of *Boleosoma nigrum olmstedii* from the upper Susquehanna River system at Candor and Willseyville, New York, collected in late fall and early spring over the period from 1925 to 1942.

Standard length in millimeters	Summers of Life							
	I		II		III		IV	
	♂	♀	♂	♀	♂	♀	♀	
24	2	
26	4	1	
28	7	7	
30	6	10	
32	12	10	
34	6	12	
36	10	8	...	2	
38	8	4	...	5	
40	2	2	3	12	
42	9	...	3	16	
44	3	...	4	19	...	3	...	
46	2	...	8	8	...	3	...	
48	1	...	12	5	...	7	...	
50	10	4	...	6	2	
52	13	3	...	2	...	
54	15	...	2	6	...	
56	8	...	4	1	1	
58	7	...	9	1	...	
60	4	...	4	
62	1	...	2	
No. of specimens	72	54	88	74	21	29	3	
Mean	34.9	32.8	51.2	43.4	58.0	48.6	...	

May. Various series of specimens taken during April showed no sign of growth. However, all the specimens in a given locality will not show an annulus at a given date. Generally it is formed slightly earlier in smaller specimens. The scales of adults show no growth until after the spawning season, which in this vicinity begins during the last days in April and the first three weeks in May. However, the beginning of the breeding season may vary slightly from year to year depending largely on the water temperature. Farther north at Fair Haven Bay, Lake Ontario, New York, the spawning season falls a little later or during the last of May. A series of *Boleosoma nigrum olmstedii*, most of which were spawning adults, were taken here on May 29, 1938, and May 25, 1941. A resumption of growth had occurred in practically all individuals although only a few new circuli were formed.

Longevity

The age of 845 specimens of *Boleosoma nigrum olmstedii* was determined and the results summarized in Tables 1 and 2. The age-frequency distributions are portrayed graphically in Figure 3. These data indicate that *olmstedii* is a

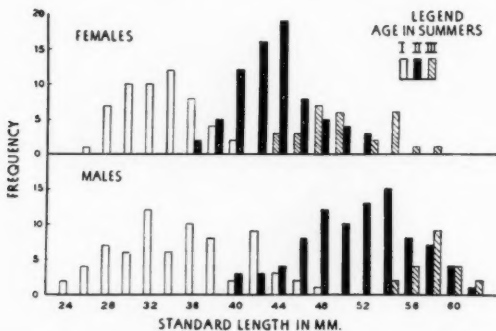


Fig. 3. Age-frequency distribution of 340 *Boleosoma nigrum olmstedii* collected in the late autumn and early spring from the upper Susquehanna River system at Candor and Willseyville, N. Y. (Table 1).

short lived species. It occasionally survives a fourth summer and winter, but, for the most part, the life span is probably concluded by the end of the third year. Only three females out of 160 examined from the Susquehanna River system had passed through a fourth summer (Table 1). At the same locality, out of 181 males examined, none had lived this long. Of these males, only 21 had lived as long as three years. It should be stated in this connection that a special effort was made to collect large specimens at this locality. The largest *olmstedii* we examined was a male 88 mm. in standard length collected by B. C. McCabe on April 18, 1942, in a tributary on the Connecticut River near Springfield, Massachusetts. It had just passed through a fourth winter. This

TABLE 2.—Length frequencies for each age group (summers of life) of 505 specimens of *Boleosoma nigrum olmstedii* from several localities in New York and Massachusetts.

Locality	Fair Haven Bay, Lake Ontario, N.Y.				Oneida Lake, N. Y.				Trib. of Miller R. Franklin Co., Mass.		Otter River, Worcester Co., Mass.			
Date	Late May, 1938 and 1941				June 21- 25, 1941		July 21, 1935		July 7, 1940		July 9, 1940			
Standard length in mm.	I +		II +		I +		I +		I +		I +		II +	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
24		1												
26					1									
28		1			1									
30		2			4			1						
32		4			12	2		1		4				
34	1	2			5	5	4	5	3	6				
36	3	1			15	5	14	16		6				
38	2	5			14	1	14	9	2	5		1		
40	7	4			17	1	19	16	4	5		6		
42	4	2		2	9	1	23	9	2	3	2	6		
44	2	2			4		20		5	1	1	12		
46	3		1		8	1	13		2	1	1	17		
48	3			3			7		2	1	3	15		4
50	2		1				3				7	5		1
52	1		3	1			2				5	1		
54	1		1								1	1	1	5
56			3								2		2	2
58			1											
60													2	
62														
No. of specimens	29	24	10	6	90	16	119	57	18	33	22	64	5	12
Mean	42.8	36.0			38.0	36.3	41.6	38.0	41.0	37.8	49.7	45.6		

is by far the largest specimen we have seen out of the several thousands of specimens examined in the field and in museum collections. Under some conditions the numbers of large *Boleosoma* may be cut down considerably by predations of game fish.

Although only 102 specimens of *Boleosoma longimanum* were available for examination, they were representative samples from large populations in nature, and it is not likely that any important changes in the picture would occur if additional specimens were to be aged. This species exhibits growth characteristics similar to those of *olmstedii*. The data are summarized in Table 3 and Figure 4. One out of 61 females examined had passed through four winters, but no male had lived this long. One male out of 41 had lived three winters.

Growth Rate

The growth data on 340 specimens of *olmstedii*, taken from tributaries in the upper Susquehanna River system in New York, are given in Table 1, and

Figs. 3 and 5. It may be seen that most growth or more than half the total, took place in the first year of life. Considerable variation in growth occurred in each age group. Males at the end of their first summer averaged 34.9 mm. (24 to 48 mm.) in standard length, while females were 32.8 mm. (26 to 40 mm.). This slight difference in length at the end of the first year is not statistically significant.

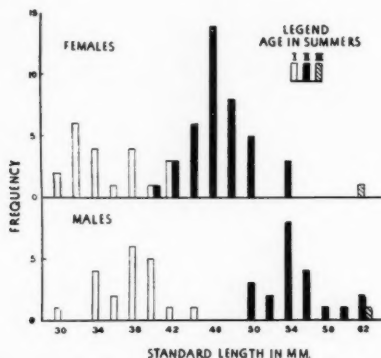


Fig. 4. Age-frequency distribution of 102 *Boleosoma longimanum* collected from March 30 to April 7, 1940 from the upper James River system, Virginia.

In both sexes there is considerable overlap when the length of those which have passed through two summers is compared with those which are one year old (Table 1 and Fig. 3). At the end of their second summer males had reached a mean length of 51.2 mm. (40 to 62 mm.), but the slower growing females attained only 43.4 mm. (36 to 52 mm.). The difference in the length of the sexes at this age is statistically significant. The faster growing males at the end of their second summer had attained a length of 62 mm., a length as great as that of any three year old female examined. Those males surviving a third summer averaged 58 mm. (54 to 62 mm.), while the females of the same age averaged 48.6 mm. (44 to 58 mm.). This difference in size of the sexes at the end of the third summer is highly significant. There is considerable overlap in the age-frequency distributions of two and three year old females. Only three females had passed through a fourth summer, and they were well within the size range of the three year old specimens. It is interesting to note that when a length-frequency curve based on the data in Table 1 is compiled for each sex, but not considering age, the females show three well developed peaks, each of which represents a point close to the mean length of an age group. When a length-frequency curve of the males was plotted, the peak of the one year old specimens was separated pronouncedly from the older males. However, the two and three year old males could not be separated from each other. The probability of inaccuracies when age is estimated from length-frequency distributions has, of course, been recognized by those who have

used them in the past (Lake, 1936; Raney and Lachner, 1938). The best that can be accomplished by this method is to separate most of the one year olds from older specimens.

Too little information on *olmstedii* is available from other localities to allow for as complete a discussion as that given above. However, some data from other places in New York and Massachusetts are summarized in Table 2. Most specimens were in their second summer of life. Older individuals were conspicuously rare or absent in most collections. These data corroborate our findings based on more adequate data given above. This is true especially in

TABLE 3.—Length frequencies for each age group of 102 specimens of *Boleosoma longimanum* from the upper James River system, Virginia, collected from March 30 to April 7, 1940.

Standard length in millimeters	Summers of life					
	I		II		III	IV
	♂	♀	♂	♀	♂	♀
30	1	2
32	6
34	4	4
36	2	1
38	6	4
40	5	1	1
42	1	3	3
44	1	6
46	14
48	8
50	3	5
52	2
54	8	3
56	4
58	1
60	1
62	2	1	1
No. of specimens	19	20	21	40	1	1
Mean	37.6	35.4	54.9	46.3

regard to the differences in growth of the sexes which shows up during the second summer. The data (Table 2) on *olmstedii* from two localities in Massachusetts, collected about the same time, indicate significant differences in growth rates.

The growth rate of *Boleosoma longimanum* from the James River system (Table 3 and Fig. 4) is very much like that of *Boleosoma nigrum olmstedii* from the Susquehanna River system in New York. Here the males averaged 37.6 mm. (30 to 44 mm.) at the end of their first year. The females grew at about the same rate and averaged 35.4 mm. (30 to 42 mm.). No overlap was found in our sample when the growth of two year old males was compared with one year old males. Two year old males averaged 54.9 mm. (50

to 62 mm.). Females in their second year did not grow as rapidly as the males and attained an average length of 46.3 mm. (40 to 54 mm.). A slight amount of overlap occurred in the length-frequency distributions of one and two year old females. Since so few specimens more than two years old were obtained under ideal seining conditions, we are inclined toward the interpretation that few specimens of *longimanum* of either sex live much beyond their second breeding season. No growth curve for *longimanum* is included since it is almost identical with that for *olmstedii* (Fig. 5).

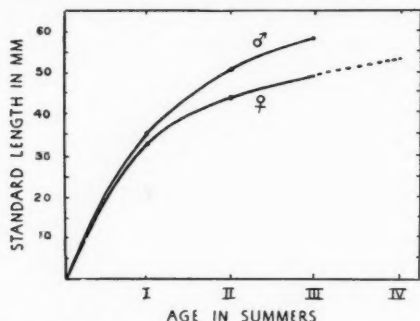


Fig. 5. Growth curve of *Boleosoma nigrum olmstedii* based on 340 specimens from the upper Susquehanna River system at Candor and Willseyville, New York (Table 1). Only three females had passed through a fourth summer (dotted line).

It has been pointed out in the discussion above that males and females of both species do not differ significantly in the size attained at the end of their first summer of life. However, there is a significant difference at the end of the second and third summers, and the males attain a larger size. A greater length is also reached by males of *Catnotus flabellaris flabellaris* (Lake, 1936: 828), *Poecilichthys maculatus* (Raney and Lachner, 1939: 164) and *Poecilichthys caeruleus* (Reeves, 1907). In *Boleosoma*, *Catnotus* and *Poecilichthys maculatus*, the eggs are laid under a stone or other similar object and are guarded by the male. In *Poecilichthys caeruleus*, the males guard certain areas and drive rival males away.

On the other hand, Petravic (1938: 40) reports that the sexes attain equal lengths in the black sided darter, *Hadropterus maculatus*. It spawns in riffles at a spot chosen by the female, and no guarding is done by the male. There is a dearth of published information on the sizes of the sexes in other darters whose breeding habits are known. However, the females are larger than the males in the yellow perch. In this species the eggs are usually laid on aquatic plants or submerged brush, and the males do not guard the nesting areas.

In conclusion it appears from the available data that in those species of darters where a territory is guarded, the males average larger than the females.

In those percid fishes not guarding nests the sexes are approximately the same (*Hadropterus maculatus*), or the females are larger (*Perca flavescens*). A parallel situation is found in at least one other family, the Cyprinidae. In those minnows which build nests, such as *Semotilus a. atromaculatus*, *Leucosomus corporalis*, *Nocomis micropogon*, *Nocomis biguttatus*, etc., the males are larger than the females. In the non-nest building minnows where the growth rates has been studied, such as *Hybognathus nuchalis regius* and *Notropis rubellus*, the females are larger than the males. It appears that a selection occurs in the nest building forms whereby the largest males are more successful in breeding and guarding the eggs until they are hatched.

The faster growing individuals of both sexes of *olmstedii* are mature and breed when one year old. All are mature and breed at an average age of two years. After spawning for either a second or third time, and when an age of three years is attained, the life span is probably ended for all but exceptional individuals. With *Boleosoma longimanum* some males and females spawn at an age of one year. All breed when two years old.

Summary

1. This study of age and growth rate was based on 845 specimens of *Boleosoma nigrum olmstedii* from New York and Massachusetts, and on 102 specimens of *Boleosoma longimanum* from the James River system in Virginia.
2. In structure, the scales are similar to those of the pike-perch. When growth resumes in the spring the circuli on the anterior field of the scales are far apart in contrast to those which were laid down during the previous fall. This was obvious from a study of large numbers of young and adults taken at one locality at different times during the year.
3. In *olmstedii* growth resumes in May in central New York. This coincides with the completion of the spawning season at many localities. Growth begins a little earlier in the smaller yearlings. In *longimanum* an annulus was already formed in early April.
4. Both *olmstedii* and *longimanum* are short lived species. The typical life span in *olmstedii* is three years, although it occasionally lives through a fourth summer and winter. Few *longimanum* appear to live through a third summer.
5. In *olmstedii* from tributaries of the upper Susquehanna River system in New York males attain a mean standard length of 34.9 mm. (24-48 mm.); 51.2 mm. (40-62 mm.); 58.0 mm. (54-62 mm.) at the end of the first, second and third summers of life. Females reach 32.8 mm. (26-40 mm.); 43.4 mm. (36-52 mm.); 48.6 mm. (44-58 mm.) in the same time. Three females lived through a fourth summer.
6. The main features of growth rate and longevity in *olmstedii* are the same in other localities in New York and Massachusetts.
7. Although the more southern species, *longimanum*, grew somewhat more rapidly than *olmstedii*, its growth pattern is similar. Males reached 37.6 mm. (30-44 mm.) and 54.9 mm. (50-62 mm.) at the end of their first and second

years, and one three year old male was 62 mm. Females attained 35.4 mm. (30.42 mm.) and 46.3 mm. (40.54 mm.) at an age of one and two years. One 62 mm. female was four years old.

8. Males and females of both species did not differ significantly in the length attained at the end of one year. Males were significantly larger at two years in both species and at three years in *olmstedii*.

9. The faster growing individuals of both sexes of *olmstedii* are mature and breed when one year old. All spawn at two years. Fewer *longimanum* spawn at one year, although all are mature when two years old.

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Additional Studies on the Movement of Tagged Bullfrogs, *Rana catesbeiana* Shaw

William Marcus Ingram and Edward C. Raney

During the summer of 1939 the movements of 237 tagged bullfrogs, *Rana catesbeiana* Shaw, were studied at the Edmund Niles Huyck Preserve, at Rensselaerville, Albany County, New York. These frogs were marked by locking numbered monel metal tags around the dentary bone. The results were reported by Raney (1940). Other studies on the growth of these bullfrogs in nature have been reported by Raney and Ingram (1940 and 1941). Additional returns on 22 individuals recaptured by Ingram in the summer of 1940, and 12 records obtained by Dr. Jean Piatt during 1941 serve as a basis for these notes.

The Edmund Niles Huyck Preserve is an area of about 500 acres situated in the Helderberg Mountains. The salient features of the terrain of interest to this problem are shown in the aerial view of the Preserve in Raney (1940: 736). Two ponds, Lincoln and Myosotis, of nine and ninety acres, respectively, and a small wooded pond, Trout Pond, are those in which the frogs were caught. The lack of disturbance by human agency greatly reduces the chance of distorted records.

Movement from Summer to Summer

The records of the distances moved by frogs released in 1939 and recaptured during the following two years are given in detail in Table 1. It is obvious that the distances traveled by certain individuals during the elapsed period between captures may have exceeded those recorded in the Table 1. The period of activity at this locality is approximately seven months, or from the middle of April to the last of October. Most of the bullfrogs that moved distances of 3000 to 3800 feet, probably followed the course of a stream flowing from Lincoln Pond to Myosotis Pond. The bullfrog that covered a distance of 5250 feet probably followed this same water-way, but near the end of his journey had to climb a hill a distance of 450 feet to reach a small reservoir. Several other frogs made short overland trips; one immature bullfrog moved from Trout Pond to Lincoln Pond, a distance of approximately 250 feet. Another immature specimen made the reverse journey from Lincoln Pond to Trout Pond. One immature individual released in Trout Pond in 1939 was found there in 1940. Seven bullfrogs released in Lincoln Pond in 1939 were recovered in 1940. One female was tagged and released in a small reservoir in 1939 and was recaptured at the same place in 1940. All twelve recaptures made in 1941 were from Lincoln Pond but no serious search was made for tagged frogs in the other ponds. No significant difference in the

TABLE 1.—Distances moved by bullfrogs which were tagged in 1939 and were recaptured in 1940 and 1941. Those in column two which are followed by an asterisk are specimens which had moved to another pond during the elapsed period.

Date released in 1939	Date recovered in 1940	Distance moved in feet	Date recovered in 1941	Distance moved from point of last release
Sept. 22	July 20*	5250		
August 2	July 17*	3800		
Sept. 22	July 17*	3500		
July 12	July 17*	3450		
August 11	July 28*	3450		
July 14	July 16*	1150		
Sept. 22	July 17*	470		
August 11	July 18	370		
July 4	July 17	280		
August 11	July 18	60		
Sept. 22	June 17	30		
July 14	June 17	20		
Sept. 22	July 20	0		
August 11	July 28	0		
July 14	July 21	0		
July 14	June 21	0		
July 17	June 16*	3000	May 19	110
August 6	July 22*	3300	May 19	470
July 12	July 17	450	May 22	0
July 11	July 18	360	June 3	100
August 28	July 19	80	May 19	650
Sept. 22	July 24	10	June 7	10
July 9			June 3	500
July 11			May 20	480
July 14			June 12	450
Sept. 22			May 19	65
August 11			June 26	50
July 14			April 17	20

distances moved by immature specimens, or by adult males or females, was apparent.

Summer Movement (1940)

These data are based on recaptures of bullfrogs during the summer of 1940. One male bullfrog released on June 16 had moved 10 feet when taken on June 17; when recaptured on July 18 it had moved an additional 675 feet; and when again taken on July 24, it had moved an additional 562 feet. Thus in the period from June 16 to July 24 the known distance moved totaled 1,247 feet. One immature bullfrog released on July 17 was recaptured on July 19, 400 feet away from the release area. A male bullfrog released on July 17 was recaptured on July 19 at a point 570 feet distant. A female bullfrog taken on July 18 was captured 675 feet away on July 20; and on July 23 was found 60 feet away from the point of last release. One immature bullfrog remained in one area from July 17 to July 19; it had moved 60 feet when it was again taken on July 24. An immature bullfrog moved 400 feet entirely overland between July 17 and July 19. The longest bullfrog movement yet to be

recorded during a single activity season was made by an individual released on July 9 and recaptured on July 28 at a point 4000 feet distant.

Homing and Spawning Season

Three instances of homing were observed in bullfrogs and add to the published observations of McAtee (1921) Breder, Breder and Redmond (1927), and Raney (1940). A female bullfrog moved 675 feet to return to the area of original capture in 48 hours; this movement was probably along a water-way. One male bullfrog was taken 570 feet across land and 48 hours later was found to have returned to the original point of capture. An immature bullfrog moved 400 feet across land in 48 hours from the release area to the original capture area.

According to Raney (1940) the bullfrog spawning season on the Preserve extended through the first three weeks in July, 1939. Observations in 1940 indicated that the bullfrog spawning season extended from approximately June 15 to July 1. The eggs of the green frog, *Rana clamitans*, were collected from July 1 through July 23, 1940.

The writers are indebted to the late Dr. G. K. Noble of the American Museum of Natural History for aiding in the field work, and to Dr. Jean Piatt, Resident Naturalist of the Edmund Niles Huyck Preserve, for making available his 1941 records.

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The Sexual Behavior of Anura. IV. Oviposition in the Mink Frog, *Rana septentrionalis* Baird¹

Lester R. Aronson

Because of certain morphological similarities, *Rana septentrionalis* is generally considered a small representative of the bull frog—green frog group (Garnier 1883, Dickerson 1906, Boulenger 1920, Wright 1932). However Cope (1889) considered that "this species occupies a position intermediate between nearly all the North American species of the genus," and he suggested that from some form such as *Rana septentrionalis* all the *Ranae* of the northern hemisphere have been derived. Wright (1932) suggested that its closest relationship is with *Rana virgatipes*.

One outstanding difference between *Rana septentrionalis* on the one hand, and *Rana clamitans* and *Rana catesbeiana* on the other is the appearance of the egg masses. The eggs of the mink frog appear as a solid mass or plinth below the surface of the water, similar to the eggs of *Rana pipiens*, and are unlike the eggs of the bull frog and green frog which are surface films.

The oviposition mechanism involved in forming a surface film is considerably different from that utilized in forming a solid mass (Aronson, 1943). It could therefore be predicted that the egg-laying process of *Rana septentrionalis* would resemble *Rana pipiens* rather than *Rana clamitans* or *catesbeiana*.

Mr. Lewis H. Babbitt of Petersham, Mass., collected 57 mink frogs during the first week in July, 1940, in the vicinity of Connecticut Lakes and Diamond Pond in northern New Hampshire, and sent them to the Laboratory of Animal Behavior of the American Museum of Natural History. The females had not yet ovulated and to initiate this process, the pituitary injection method of Rugh (1935) was used. With a limited supply of homoplastic implants we were not successful in inducing the females to ovulate. Shifting to *Rana clamitans* pituitaries, we succeeded in obtaining three fully ovulated females, all of which were clasped by implanted males. However, only one oviposition was witnessed.

The female whose oviposition was seen received one homoplastic pituitary on July 9, 1940, one on the following day and three *R. clamitans* pituitaries on the third day. The male received one *R. septentrionalis* pituitary on each of the first two days and one *clamitans* pituitary on the third day. Oviposition occurred four days after the injections were started, and took place in a 15 gal. aquarium containing 3 inches of water.

¹ This study was supported by a grant from the Committee for Research in Problems of Sex, National Research Council.

Pre-oviposition activity in *Rana septentrionalis* consisted of periods of active swimming interspersed with periods of backward shuffling movements. The latter consisted of peculiar shuffling motions of the hind limbs which tended to move the female backward. These movements appeared very similar to those already described for *Rana pipiens* (Noble and Aronson 1942). The pre-oviposition activity lasted about three hours. As the time for egg laying approached, the hind limbs of the female began to form, during the backward shuffling, a diamond-shaped enclosure for the reception of the eggs. The female assumed this position several times before the actual onset of the oviposition. During this pre-oviposition period only two minor differences were noted as compared with *Rana pipiens*. First, the periods between backward shuffling in *R. septentrionalis* were mainly utilized by swimming activity, while *R. pipiens* during this period usually rested quietly. Secondly, the hind limbs of the clasping male *R. septentrionalis* were not as tightly flexed as were those of *R. pipiens*.

The oviposition was initiated by the female. She ceased backward shuffling and held her hind limbs so as to form the diamond-shaped enclosure. Her thighs were extended outward and backward at approximately a 45° angle, with knees resting on substratum. Her legs were turned in at approximately the same angle; the tarsi were raised above the substratum, pointing caudally and inward, and almost touching each other, while her toes rested on the substratum, pointing outward and cephalad.

As the female assumed the above posture, the male flexed his hind limbs, his thighs extending outward almost at right angles to the body axis. Within one minute the female contracted her abdominal muscles sharply and arched her back concavely. A small mass of eggs issued from her cloaca. Apparently stimulated by these movements (Noble and Aronson 1942) the male followed a fraction of a second later by arching his back convexly, which caused his cloaca to slide slightly forward. At this time the male's legs moved slightly forward while his feet turned out a little. These movements have been termed the upstroke.

The downstroke which immediately followed was initiated by the female who straightened out her arched back. Again this was followed by the male who straightened his arched back, moved his legs somewhat posteriorly and turned in his feet slightly, rotating them at the ankles.

The above motions were repeated until all the eggs were laid. The egg laying took almost ten minutes. The female then moved out of the egg-laying posture and away from the egg mass while the male released his clasp upon the female.

The eggs proved fertile and tadpoles were raised. In comparing this oviposition with that of *Rana pipiens*, the only difference observed was the position of the thighs of the male which in *Rana septentrionalis* are pointed more outward than in *pipiens*. Thus, comparisons of the egg-laying process present additional evidence indicating that the mink frog is not as closely related to the bull frog and green frog as some previous workers have suggested.

Although sufficient material was not available to make a study of the mechanism of sex recognition, and the discrimination by the male of the ovulated from the non-ovulated female, preliminary observations indicated that these processes did not differ materially from those described for *Rana pipiens* (Noble and Aronson 1942). The warning croak and small girth appear to cause the male to release his clasp. Moreover the warning croak which is distinct in a non-ovulated female disappears after ovulation.

Summary

1. By means of homoplastic and heteroplastic pituitary injections, sexually active males and ovulated females were obtained, and one complete oviposition of *Rana septentrionalis* was witnessed.

2. The pre-oviposition activity and the egg-laying process differed from *Rana pipiens* in only a few minor details. These data present additional evidence against a close affinity with *R. clamitans* and *catesbeiana*.

3. Preliminary observations indicated that the sex-recognition mechanism was similar to that of *Rana pipiens*.

The author wishes to acknowledge the assistance of Miss Arline Douglass in making the observations, and expresses his appreciation to Dr. Frank A. Beach for reading and criticizing the manuscript.

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Another Analysis of the Status of the Western King Snakes of the *Getulus* Group

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In an article, "The California King Snake, a Case of Pattern Dimorphism," (*Herpetologica* 1:18-27, figs. 1-2, 1936), Klauber presents evidence from which he concludes (p. 26):

Lampropeltis californiae (Blainville), 1835, a striped king snake of southern California and northern Lower California is shown to be a pattern phase, rather than specifically distinct from the common ringed king snakes of the Pacific Coast hitherto known as *Lampropeltis getulus boylii* (Baird and Girard), 1853. The combined form must be known as *Lampropeltis getulus californiae*. The proof of identity was secured by hatching broods which contained both forms. By analogy *Lampropeltis nitida* of the Cape region of Lower California is thought to be a pattern and color phase of *Lampropeltis getulus conjuncta*, but this in turn is of doubtful validity so that all of these king snakes should be referred to as *L. g. californiae*.

More recently another article, "A Further Study of Pattern Dimorphism in the California King Snake" (*Bull. Zool. Soc. San Diego* 15:1-23, figs. 1-7, 1939), by the same author, presents still further evidence which is believed to support the general foundation of the previous conclusions. Klauber summarizes this paper as follows (pp. 21-22):

A further investigation of the peculiar pattern dimorphism evident amongst the king snakes of the San Diegan region of southern California belonging to the subspecies *Lampropeltis getulus californiae* indicates that five pattern types are in evidence. Two of these comprise about 90 per cent of the population. The other three are intermediates, two of them being sex-linked. A mother of any phase can produce young of any other phase, but tends to produce a high proportion of young of her own phase. Broods hatched in captivity are found to have a higher percentage of aberrants than the general population, indicating a probable high mortality amongst aberrants. Pattern phases are not correlated with differences in lepidosis.

The power to produce the major pattern variant is restricted to a relatively small area within the range of the subspecies. On the periphery of this area the atypical specimens are reduced in number and are imperfect in the nature of their deviations, somewhat resembling a small proportion of mixed specimens in the central area. Beyond this periphery there is a much larger area inhabited by the same subspecies but in which there seems to be no power to produce any of the atypical patterns.

Modifying Klauber's taxonomic conclusion somewhat (in accordance with a suggestion of Klauber's), Perkins, in his "A Key to the Snakes of the United States" (*Bull. Zool. Soc. San Diego* 16:36, 1940) uses the name *getulus californiae* for specimens "found in the territory where striped or aberrant phases are found," and the name *getulus boylii* for specimens outside of that territory.

That this extraordinary situation, whose aspects have been clarified almost solely by Klauber's work, should stimulate discussion and perhaps some dissension is to be expected. Although Klauber's taxonomic conclusions (and Perkins'

modification) may well be correct, worthy of equal consideration are other aspects which furnish strong arguments for a different viewpoint: i.e., that *californiae* must be considered a species distinct from *getulus boylii*. Radically different as this viewpoint is from Klauber's, it has much in its favor; on the whole, I believe it the more logical expression of the status of these snakes. The following discussion may present some support for this belief. I am indebted to Dr. E. H. Taylor, Dr. H. H. Lane, Dr. Sherman C. Bishop, and especially to Dr. Curt Stern for their generosity in reading and criticizing this discussion.

That the *californiae* pattern has been derived from a *boylii*-like pattern seems a fairly certain conclusion. The arguments supporting this contention are several. First, *californiae** is like *boylii* in scutellation (both different from certain others of the *getulus* group) and therefore is probably of no great age, yet the only ancestors from which it may have arisen in comparatively recent times are ringed; the entire *getulus* group, to which *californiae* belongs, shows various stages in the development of the ringed pattern. Second, *californiae* is contained entirely within the range of *boylii*. Third, intermediate specimens in which the pattern only of the extremities is modified have a midbody pattern of the ringed type (this is of significance since the midbody pattern very probably is more static than the pattern of the extremities, where modifications appear to be initiated).

It may be granted that *californiae* is of relatively recent development. In addition it must be granted that *californiae* is not of the same character as the races of *getulus*. It is not territorially distinct, does not blend uniformly with the geographically adjacent races (in this case, the coincident race), and is much more radically different from its relatives than the latter are from each other. This peculiar character of *californiae* may have been effected by (1) isolation over a very long period; (2) sudden mutations involving some factor causing partial isolation from a geographically coincident parent stock; or (3) a temporary isolation followed by a confluence with the parent stock.

That *californiae* has not been differentiated during a long period of isolation is indicated by the arguments presented above. It may well have arisen by either of the other two methods, and which of the two is more probable is difficult to prove. If, however, *californiae* is a product of sudden mutation (2), it is reasonable to assume that it is a new form spreading outward from its apparent point of origin (San Diego county). On the other hand, if *californiae* is a product of temporary isolation, it is reasonable to suppose that it may be in the process of suppression. This supposition seems the more probable because of (1) the apparently greater proportion of ringed or aberrant young produced by striped or aberrant mothers than striped or aberrant young produced by ringed mothers. Moreover, (2) the actual proportion of pure striped to pure ringed specimens in the area of greatest abundance of the former does not indicate that it is a dominant type (a maximum ratio of 40% striped to 54.3% ringed, the remainder intermediate). Finally, (3) the area occupied by

* Used in this paper only in reference to the striped specimens.

californiae at present is much smaller than the area it probably would cover lacking competition with *boylii*; very possibly it once extended about to Lat. 31° in Baja California, northward to Los Angeles and Riverside counties, and eastward to the Salton Sea, as these are the approximate limits of a biotic area once somewhat isolated and still evidenced in the distribution of many animals. Still other arguments, based on the evidence afforded by Baja California forms, are discussed below in the treatment of the southern forms. On the whole, therefore, the temporary isolation and subsequent confluence theory seems the most probable one to account for the differentiation of *californiae*. A somewhat longer isolation than actually occurred perhaps would have permitted a complete physiological differentiation of the two species, so hybridization after coalescence could not have occurred. But in either case, it is apparent that free interbreeding of the *boylii* and *californiae* phases does not occur, else the hybrids would occur in a much greater proportion. Obviously there is a very nearly complete physiological isolation of the two types where they occur together in the nearest approach to the pure state.

In other words, we are dealing with two populations, one occurring entirely within the range of the other, and which are not, considered together, populations "freely interbreeding and maintaining a high degree of constancy in most superficial as well as in all fundamental details throughout a generally considerable area" (Blanchard). Obviously we are not dealing with a single population, but rather with two species, or subspecies as circumstances demand. The situation is not the typical subspecific one, at least as geographic races are usually considered. In fact by definition a subspecies is a population which freely interbreeds and undergoes a complete protoplasmic exchange, in intermediate territory, with a different, associated population which is geographically, ecologically or otherwise segregated. In the present case such a complete exchange would probably result in prompt loss of identity of the two types and a uniform diffusion of the new characters throughout the whole area occupied by the parent population. Therefore we are faced with the necessity of calling *californiae* a species different from *boylii*, and admitting the occurrence of a very limited amount of crossing resulting in rare hybrid* specimens (5.7 % of the total population), which show a partial mixing of the two species.

This accounts satisfactorily for the central area (largely San Diego county) where the striped specimens exist in a modern concentration and do form a true, partly pure population. However, in adjacent areas hybrid specimens showing all degrees of variation between the extremes represented by *californiae* and *boylii* occur with much greater frequency than specimens pheno-

* It is of importance in this connection to note that nearly half of Klauber's "aberrant" specimens, all of which he calls intermediate, belong to *californiae* and cannot be considered intermediate between *boylii* and *californiae*; these are the ones with a dark venter. This character is found only in *californiae* (predominantly in females), never in *boylii*, and specimens bearing the character should not be confused with true intermediates between the defining characters of *boylii* and *californiae*. Thus *californiae* has not only the striped pattern to identify it, but also, occasionally, a black belly, and, invariably, a black subcaudal area.

typically *californiae*. In fact there is an average gradient in hybrid characters which demonstrates an approach to *boyllii* peripherally, and near the periphery specimens phenotypically *californiae* never occur. Therefore there is no true population of *californiae* in most parts of the peripheral areas; only hybrids represent it and may indicate the existence in the past of pure *californiae* in these areas. It appears obvious that, in order that these hybrids maintain themselves over more than two or three generations, there must have been a dilution of the character causing the nearly complete physiological isolation of the two species, at the same time that there was a dilution of the *californiae* characters. And in order to account for the dominance of *boyllii* rather than *californiae* characters in the peripheral hybrid area, it may be assumed that, for unknown reasons, back-crossing of the hybrids with *boyllii* rather than with *californiae* may be favored to some extent and that the *boyllii* characters are at least partially dominant.

Now if such has been the procedure, it may be asked why the process has not proceeded at all points with equal rapidity, rather than being concentrated in peripheral areas that appear to converge in a central area where little crossing has taken place in spite of the dominance in numbers of apparently pure *boyllii* (5.4) over apparently pure *californiae* (4). It seems necessary to conclude that this process does occur with equal rapidity at all points, and that the peripheral disappearance of phenotypically pure *californiae* and its survival only in a small central area are correlated with some type of selective evolution and "survival of the fittest," wherein *boyllii* is in general better adapted to all conditions than *californiae*. The process of domination of *boyllii* over *californiae* accordingly appears to be entirely independent of the hybridization phenomena which is simply a complication of the picture made possible by an incomplete (although very nearly complete) evolution of the physiological barrier between the two species. Had the barrier been completely evolved, and thus hybrids had never been possible, by this view *boyllii* still would have dominated and encircled *californiae*. The ultimate and imminent extinction of *californiae* by *boyllii* seems to be strongly indicated.

The additional evidence furnished by the Baja California races of the *getulus* group is of great interest. Obviously *nitida* is rather like *californiae*; Blanchard considered them races of a single species. If Blanchard's assumption were correct, a corollary would be that at some time the stock which gave rise to *nitida* and *californiae* was continuous in its distribution and extended more or less the full length of Baja California. That this is not exactly true we know not only because typical *boyllii* occurs in northern Baja California, but because a population (*conjuncta*) very much like *boyllii* occurs in central and southern Baja California. It is of course possible that *boyllii* may have migrated into Baja California at the end of the period of isolation, replaced *nitida* as it moved southward, became extinct in north-central Baja California (between Comondú and Rosario), and then became slightly differentiated in the southern and central parts of the peninsula, but this seems very highly improbable. Much more probable seems the possibility that all of Baja California as well as southern California was at one time occupied by a stock like

boylii, and that at the time the population that became *californiae* was isolated in the north, the population that became *nitida* was isolated on the Cape. As has been indicated, *nitida* evolved a pattern similar to that evolved by *californiae*, yet these two are not as closely related to each other as the latter is to *boylii*, and the former to *conjuncta*; the partial parallelism in pattern evolution is not surprising in view of the common orthogenetic trend of the common stock from which they were derived. The population in central Baja California (now *conjuncta*) probably remained in contact with that in the north (now *boylii*) by the Sierra San Pedro Mártir, or by the area east of this range; if such contact had not been maintained the central population probably would have become differentiated as were *nitida* and *californiae*. Regardless of the reason, the central population ultimately became but little modified from *boylii*; it has become slightly modified at least, probably due to a presumably recent separation in the area between Comondú and Rosario. As the Cape region became united again with central Baja California, *conjuncta* migrated southward and now occurs in the Cape region with *nitida*, while the latter, like *californiae*, apparently has been unable to extend its range. Whether *nitida* is undergoing hybridization with *conjuncta*, as *californiae* is with *boylii*, is not now evident, but in any event it is obvious that *nitida* is no more successful in direct competition with its ancestor than *californiae* is with its ancestor. In the absence of more conclusive evidence, it seems best to treat *nitida* like its analogue, *californiae*, and retain it as a species distinct from *getulus conjuncta*.

The isolated *catalinensis* on Santa Catalina Island in the Gulf of California is of great importance. It may be supposed that it was isolated at the same time as *nitida* and *californiae*, and that it has not been subjected to a subsequent competition with the parent stock as have *nitida* and *californiae*. In fact, it will be of the greatest importance to learn whether *catalinensis* is the only king snake of Santa Catalina Island; if it is, then both the theory of the specific status of *californiae*, *nitida* and *catalinensis*, and that of differentiation of the striped (and nearly unicolor) species by means of recent isolation, will seem well founded. On the other hand, if a form like *boylii* occurs with *catalinensis*, neither theory would account for or be supported by its presence there; in such case at least most aspects of Klauber's theory would receive almost conclusive support. Accordingly this island may well hold the key to the western king snake problem, and its thorough exploration should be of the greatest interest.

The evidence considered above, although admittedly incomplete, appears to support strongly the following arrangement of the western king snakes of the *getulus* group:

Lampropeltis getulus boylii (Baird and Girard), 1853.

Lampropeltis getulus conjuncta Cope, 1861.

Lampropeltis californiae (Blainville), 1835.

Lampropeltis nitida Van Denburgh, 1895.

Lampropeltis catalinensis Van Denburgh and Slevin, 1921.

In addition, the existence of *L. californiae* (Blainville) \times *L. g. boylii* (Baird and Girard) hybrids is recognized.

To return to the extraordinary pattern change from the ringed pattern of *boylii* to the striped one of *californiae*, if the theory of temporary isolation (of the population becoming *californiae*) and subsequent confluence (with the parent population *boylii*) is correct, why has such an apparently radical change occurred, in such a relatively short time, when other changes in the *getulus* group have been so relatively minor? The reasons may be several, but among them it may be suggested that the next step beyond the perfect definition of the rings or blotches, in the evolution of snakes developing such a pattern, is frequently a shattering of the rings or blotches to produce stripes. The *getulus* group, in its evolution, started with a nearly uniform pattern (like *brooksii* ?); light spots developed on various dorsal scales, and then concentrated in vague transverse lines (*niger*), then cross-bands (*splendida*), later rings (*yumensis*), and finally the ring evolution reached its ultimate perfection in *boylii*. What evolutionary step beyond perfection of the rings can be taken in the progressive orthogenetic series exemplified by the *getulus* group? Obviously the light rings could increase in size at the expense of the black, or any one of several other possible types of modification (witness *catalinensis* and *nitida*) could occur, but equally as possible as any other is the formation of lateral and dorsal stripes, or both, resulting from or in a partial or complete shattering of the rings. Obviously the latter has been the procedure in the western king snakes, and accordingly the development of the imperfect striped pattern of *californiae* from the perfected ringed pattern of *boylii* need not be considered such a radical step as it superficially appears. It forms a very logical and necessary step, no more important than the other, less marked steps, in the continuous evolution of the pattern beyond the stage of completion of the rings, and development from the latter of the striped pattern.

The existence of this example, in *californiae*, of a link between the ringed and striped patterns so characteristic of snakes adds another bit of evidence to the general theory that in snakes the ringed or blotched pattern is more primitive than the striped pattern, and that the latter is directly developed from the former by a shattering of the rings or blotches. Many groups of snakes give very clear support to this theory. In addition to that given by the *getulus* group of *Lampropeltis*, may be mentioned (1) the fact that stripes are formed in aberrant specimens of the blotched *Elaphe obsoleta* and *laeta*, and typically in adults of the related *quadrivirgatus* and *bairdii*, both members of a genus typically blotched; (2) that the most primitive species (*phenax*) of a typically striped genus (*Thamnophis*) is blotched, certain specimens showing a staggering and splitting of the blotches to produce a median and two lateral stripes; (3) that "the pattern in *Dryadophis* . . . has passed from the banded type through the striped condition and has in 2 instances progressed to the unicolor form" (Stuart, Misc. Publ. Mus. Zool. Univ. Mich., no. 49, 1941, p. 32); and (4) that in *Masticophis* the most primitive form is blotched (*mentovarius suborbitalis*) and gave rise to the striped series (present *m. mentovarius*, *bilineatus*, et. seq.) as well as to the blotched series (*flagellum* and its subspecies, most with pattern visible only in the young). The list of examples could be extended greatly.

Conclusions

It is reasoned that *californiae* is a striped species relatively recently evolved, during a period of isolation, from a parent stock similar to *boylii*; that subsequent to the removal of the barrier between the ranges of the two species, *boylii* has migrated throughout the range of *californiae*, the two occasionally hybridizing; that the hybrids interbreed and back-cross with *boylii* with greater freedom than either parent interbreeds with each other or than the hybrids back-cross with *californiae*, producing a greater variety of hybrids; that *boylii* genes are partially dominant over *californiae* genes; and that *californiae* is rapidly approaching extinction through a completely independent process of competition with the more successful *boylii*.

It is reasoned that *nitida* and *catalinensis* are species that parallel *californiae* somewhat in pattern evolution, and that like it became differentiated during a period of isolation from a common parent similar to present *boylii*; that the parent stock in Baja California, having become somewhat differentiated from *boylii* by a more recent, secondary isolation, has invaded the range of *nitida* upon removal of the barrier between them, just as *boylii* invaded the range of *californiae* (hybridization indefinite); and that the parent stock has never had an opportunity to mix with *catalinensis*, since the barrier between Santa Catalina Island and the mainland has not been removed since it was formed, contrary to the situation in the other two cases.

It is suggested that the pattern evolution of *californiae* offers further evidence in support of the theory that striped patterns are evolved from blotched or ringed patterns, and that the latter are primitive patterns; this is the case in many of at least American colubrids.

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An Unusual Food-Reaction of *Chaos chaos* Schaeffer

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The generalization has been made by workers in the Miller School of Biology¹ that amoebas have a twofold manner of reacting to food, depending upon whether the food had the power to escape or not. Hyman² has recognized this generalization as valid for she says, "Lobopods and filopods employ circumfluence in the ingestion of immotile prey but capture active prey by *circumvallation*, i.e., by throwing out a wide food cup that embraces the prey without touching it and includes a large amount of water. The behaviour thus varies according to the type of food and other circumstances."

It remains to be pointed out, however, that no two reactions to food-organisms that present the contingency of escape are identical.

The following observation indicates how sustained and variable the reaction may be to an animal that endeavors to escape.

A large specimen of *Chaos-chaos* was placed into a hanging drop of filtered aquarium water and allowed to remain without food for 18 hours. Two large paramecia (probably *P. caudatum*) and a *Spirostomum ambiguum* about 2.5 mm. long were then placed into the hanging drop and the animal observed periodically for 24 hours.

The chaos engulfed both paramecia by extending pseudopodia within 15 minutes after they had been placed into the hanging drop. Then the animal remained comparatively inert for 24 hours. At this time, the spirostomum was observed to approach the chaos along the path indicated by the arrow in Figure 1. It made contact with the side of the chaos gliding through the crotch formed by two lower and one over-arching pseudopodia. By the time it had glided slightly along the chaos to the region *b*, Fig. 2, the chaos had elongated the three existing pseudopodia and extended a fourth (Fig. 2, *c*). The extension of the pseudopodia caused the spirostomum to glide posteriorly until it once again established contact with the chaos at point *a*. However, in doing this

¹ KEPNER, WM. A. AND WM. H. TALIAFERRO. 1913—Reactions of *Amoeba proteus* to food. Biol. Bull. 24.

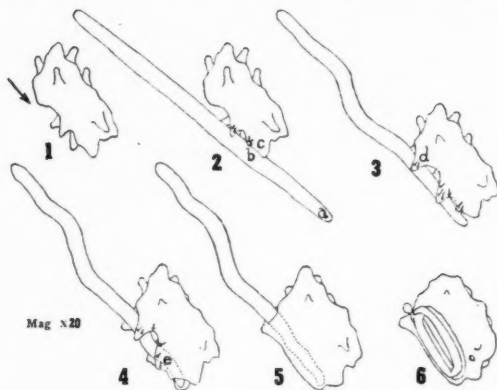
— AND J. GRAHAM EDWARDS. 1917—Food-reactions of *Pelomyxa carolinensis* Wilson J. Exper. Zool. 24.

— AND W. CARL WHITLOCK. 1921—Food-reactions of *Amoeba proteus*. J. Exper. Zool. 32.

LOOPER, J. B. 1928—Observations on the food-reaction of *Actinophrys sol*. Biol. Bull. 54.

² HYMAN, L. H. 1940—The Invertebrates: Protozoa through Ctenophora. McGraw-Hill Book Company, Inc., New York and London, p. 122.

it touched the chaos at a second point slightly posterior to the first. This contact caused the chaos to extend two more pseudopodia, one under and one over, at the second point of contact (Fig. 3, *d*). The six pseudopodia, involved in the reaction, now appeared to bring definite prehensile pressure upon the spirostomum, for it vigorously twisted and undulated its body without being able to retreat from the embrace. As the ciliate struggled to free itself, the original four pseudopodia became wider as well as longer until there was finally a fusion, forming a broad pseudopodium above and one below the spirostomum



(Fig. 4 *e*). As the specimen was thus held, the pseudopodia further widened and fused to form a deep, narrow foodcup about the victim (Fig. 5). Two-thirds of the ciliate's body extended beyond the mouth of the food-cup. The amoeba's grip was now released. The spirostomum, under its ciliary activity, then advanced anteriorly toward the fundus of the cup. Here its advance was deflected in such a manner that it doubled back on itself and swam toward the opening of the cup, pulling more of its body into the amoeba. The opening, however, was closing rapidly and proved to be too small to permit two thicknesses of the ciliate to pass, and once again the advance of the spirostomum was deflected. This advance was maintained until the long body of the spirostomum was coiled upon itself within the now widened food-vacuole, with only a posterior tip projecting from the constricting mouth of the vacuole (Fig. 6). This projecting tip was eventually abstricted. It managed to escape, but not before the amoeba had sent pseudopodia out in an attempt to gather it in. The ingested spirostomum was reduced to a small residual mass within twelve hours.

This is an interesting example of a three-fold food-reaction of *Chaos chaos*. The first phase involved the formation of pseudopodia about the advancing ciliate. The second phase was concerned with the growth and fusion of these pseudopodia to form prehensile sheets of cytoplasm that held the victim in a

firm grip. The third phase showed the formation, through further fusion of the pseudopodia, of a food cup and the releasing of the victim. The release of pseudopodial tension allowed the spirostomum to enter the food-cup under its own ciliary activity as the mouth of the cup slowly closed.

This reaction, on the part of *Chaos chaos*, has been highly variable, involving both circumfluence and circumvallation. Both types of reaction having been called upon to effect the capture of the spirostomum.

Hence not only must the variability of food-reactions to motile food-organisms be emphasized, but also the "direction" that was evident in the sustained efforts to meet a contingency. It is this "direction" that is indicated as being peculiar to vital reactions. Goldstein³ says, "But if the life of an organism consisted merely of an interplay of elementary factors which kept each other in check, how could any movement and dynamics enter into the situation to give *direction* to behavior? And direction is what we actually find as the outstanding characteristic in performance of an organism." Hopkins⁴ also remarks "That each isolated event on the other hand partakes, at least, of the nature of the whole organism. Even if it is but a single specifically catalyzed biochemical reaction it remains an event *controlled* and *directed*."

One may say then, that outside an amoeba there are random forces at play, while inside an amoeba there are *directed* forces at work.

³ GOLDSTEIN, KURT. 1939—The organism, a holistic approach to biology derived from pathological data in man. p. 88. American Book Company, New York and Cincinnati.

⁴ HOPKINS, SIR FREDERICK GOWLAND. 1936—The influence of chemical thought on Biology. Science. 84:260.

BOOK REVIEWS

THE VERTEBRATE EYE AND ITS ADAPTIVE RADIATION. By Gordon Lynn Walls. Cranbrook Institute of Science, Bloomfield Hills, Michigan, 1942. vii + 785 pp., 197 figs., frontispiece, 1 pl. \$6.50.

Adaptive evolution and biological anatomy form the core of this elaborate work on the vertebrate eye. But the book really accomplishes three major things: it serves as a manual compounding information on the eyes of all groups of vertebrates; it interprets ocular structure in terms of the natural history of animals, and it adds a significant chapter to vertebrate phylogeny through the detailed comparative anatomy of this organ. It is arranged in three sections. The first deals with basic concepts of structure, development, and visual process. The second, termed ecologic, treats of adaptive modifications to nocturnal and diurnal conditions, and, most difficultly, the two in combination, and of adjustments for various media and substrates and for the sensing of photic quality. The third reviews comparatively and phyletically the situation in the several vertebrate classes. The bibliography necessarily is but partial; it is, however, carefully selected to contain the most important sources. A novel combination of index and glossary is partly alphabetical and partly phyletic in order, and probably thereby tries to accomplish too much in one treatment; at least some trouble was encountered in using this section.

Rarely have I read a book which seemed so thoroughly worth-while in assemblage of subject content, new interpretation of anatomical and physiological data and in stimulative speculation. It touches on widely different lines of research such that its varied readers in subjects well known to them are bound to find pronouncements and some acceptance of facts with which they can justly take issue. We have found just a few such things, but they usually have been unimportant and are so scarce as in no way to mar the book or detract from its main theses. The author has a true sense of values in such lines as vertebrate phylogeny, natural history, evolutionary mechanics and psychology, apart from his own specialty of ophthalmology. The style of writing is clear, and is leavened at intervals with jocular remarks that usually, if not always, are apropos. Many of the illustrations are original, or if not are neatly reworked from those of earlier authors. With their detailed legends they frequently give in themselves a whole comparative account or outline a developmental process. Tabulations, easily read by reason of adequate spacing and large printing, handily sum up occurrences of such things as tapeta lucida, foveae, types of accommodation, and intraocular filters.

If there is any general criticism of the writing from the standpoint of a naturalist, it is the not uncommon grouping of species of diverse habits in one covering statement. Thus all owls, by implication at least, are often classed as nocturnal. We encounter references to the cat, as though there might be only one kind of cat—a time-honored manner of reference but not good natural history. In other places Walls shows clearly that he is aware of the pitfalls entailed in such treatment; probably this form of statement is dictated by desire to be concise and by lack of information in the literature on the eyes of more than a few members of a group.

After a protracted and interrupted reading of the book, some parts persist more sharply in memory than others, doubtless by reason of their especially favorable impress. I liked the argument developed on partial decussation of the optic nerve fibers from which it is concluded that the arrangement is not causally related to fusion of images from the binocular field, since, he claims, some forms other than mammals have fusion without partial decussation. Instead the partial decussation is an element in the mechanism for conjugated eye movements which are peculiar to mammals.

The exposition of the Young-Helmholtz theory of trichromatic vision seems especially useful as also the picture of the duplex retina and its relation to photomechanical

changes in the cells of this area; another good treatment is that on the functions of the fovea.

Complete reversals of evolutionary trends have been a common thing with the eye. Loss of mechanisms have many times been followed by evolution anew of almost the same devices when adaptive needs have arisen. But in other instances bizarre devices have been formed in lieu of structures apparently irretrievably lost in the course of phylogeny. The book is replete with accounts of neat adaptational arrangements such as that in the fish with four eyes (=four pupils), one set for vision in air, the other for water as the animal swims along the surface. Another instance is a seal's eye which combines marked astigmatism with an appropriately arranged slit pupil in order to see in the air as with a pin-hole camera; beneath the surface of the water the astigmatism is lost and the pupil is greatly enlarged to take in as much light as possible. Then there is the tree-snake provided with what amounts to a telescopic sight for aiming at its prey; it consists of increased acuity due to a fovea placed so as to be illuminated through a peephole slit at one side of the pupil.

Finally a major idea is implanted in the reader's mind: The eye has not only evolved elaborately itself but has had a great influence on adaptive trends of the vertebrate subphylum as a whole. Locomotion of vertebrates has been said to be a key to their evolution. "If nothing on earth moved, there would never have been such things as eyes" (p. 343). But one realizes that the evolution of locomotion and the conquering of new media has been modified by the ability and limitation of the eye in evolving an effective sensory mechanism to guide the movement. Walls' book goes a long way to show how this relationship works out.

The author and the publishers are to be commended on producing a book of such high quality, one which we predict will be enthusiastically received and widely used as a standard reference by this generation of zoologists.—ALDEN H. MILLER, University of California, Berkeley, Calif.

HANDBOOK OF FROGS AND TOADS. THE FROGS AND TOADS OF THE UNITED STATES AND CANADA. By Anna Allen Wright and Albert Hazen Wright. Comstock Publ. Co., Ithaca, N. Y., 1942. xi + 286 pp., 88 pls., 7 figs.

The reviewer's heart is warmed as if by some magic as he remembers Dr. Albert Hazen Wright standing knee deep in the cold waters of the Inlet, at one end of a seine, and lecturing to a group of much less hardy and shivering students on the bank. Sherman Bishop perhaps, perhaps sometimes the reviewer, may have stood at the other end of the seine. This lecturing with the very fish or frog in hand is outdoor teaching in the best Agassizian tradition. There is a happy parallel between this recollection and the present book, in which the authors appear to stand veritably in the midst of a living stream of the tailless amphibians of North America. They have pictured these creatures from life with their cameras, and have added still further to the vividness of their accounts of the whole list of species of frogs and toads by their wealth of quotations from their colleagues who have joined them in the study of the natural history of these creatures. Most important of their quotations are those from their own notebooks, kept in nearly every corner of the United States during the past twenty years. Future herpetologists will add Mrs. Anna Allen Wright to the list of distinguished American women herpetologists to whom the Wrights' book is so appropriately dedicated. The book is on the one hand a stimulus to the study of the frogs and toads as a part of the rich American fauna, and on the other, by its aid to identification and its extensive regional bibliographies, will promote further scientific studies of these creatures, so many of which are important in a vast network of biological research.—KARL P. SCHMIDT, Field Museum of Natural History, Chicago, Ill.

